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OF

The New York State College of Forestry

AT

SYRACUSE UNIVERSITY

SAMUEL N. SPRING, Dean

Technical Publication No. 40

A CONTRIBUTION TO THE BIOLOGY OF FOMES PINI (Thore) Lloyd (Trametes Pini [Thore] Fries)

BY

W. CLEMENT PERCIVAL

Published Quarterly by the New York State College of Forestry at Syracuse, New York. Entered as second-class matter October 18, 1927, at the Post Office at Syracuse, New York, under the Act of August 24, 1912

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HISTORY

Fomes pini (Thore) Lloyd is one of the most destructive fungi in the coniferous forests of New York State, and probably in the entire United States. Because of its large number of hosts and its common occurrence throughout the northern hemisphere, it is of great economic importance in the forest industry (5, 13, 27, 69).

As far back as 1874, Robert Hartig (37) recognized its importance and first described the now generally accepted relationship between this fungus and its hosts. Later, he not only gave detailed descriptions of the effects produced in the hosts but also recommended certain control measures (38). The principal points emphasized were, first, the avoidance of fresh scars which expose heartwood; second, the removal of diseased trees; and third, the cutting of timber before it becomes overmature.

The measures of control recommended by Hartig were later sponsored by Alfred Möller (58). He stressed, particularly, the removal of all diseased trees and the cutting off of the fruiting bodies. From Möller's reports (59, 60), it would seem that this method did not meet with very satisfactory results even in the well regulated forests of Germany. In this country, Meinecke (56) states that trees infected with the ring-scale fungus should not be tolerated in the forest and Munger (63) recommends the cutting of all insect infested and conky trees. Where the majority of the forested areas in a large region are under the control of a single government, as they are in Germany, a uniform policy of forest sanitation may prove helpful. However, this means of control seems useless in a country where it is impracticable to remove the sources of infection over large geographical units.

Another of Hartig's control recommendations, that is, regulation of the cutting cycle based on pathological data, has apparently never been tried. Some data have been presented by Boyce (14), Schmitz (70), and Day (21), which contribute to a scientific foundation for this type of control. In several of these studies, decay caused by *Fomes pini* was of first importance. Martin (53) and Hemmann (41) have indicated that a rotation of 100 years would be favorable for *Pinus sylvestris* L. in Germany. Munger (62) considered Douglas fir as comparatively free from decay until 150 years of age. Data given by Boyce (14) show that decay in this species is not an important factor until an average age of 184 years has been reached. He believes that, in the future, Douglas fir stands will be operated on a rotation of less than 110 years and, hence, the loss through decay will be small.

Mason (54) considered that *Pinus monticola* D. Don attained a maximum yield at an age of about 100 years, after which the

trees are subject to damage by fungi and insects. Weir and Hubert (81) state that an age class between 101 and 120 years presents, insofar as the data show, favorable figures upon which to determine a pathological felling age.

The third control method recommended by Hartig (38) referred to the avoidance of fresh scars which expose heartwood. Hartig had shown that the decay caused by *Fomes pini* spreads rapidly in the heartwood of the stems of inoculated *Pinus sylvestris* but that in no case did the decay enter the sapwood. From this, he deduced that the hyphae would not penetrate the sapwood of a broken branch stub and hence those stubs which exposed no heartwood could not serve as a court of entry for the red-rot fungus. The results of inoculations of *P. sylvestris* by *Fomes pini* were confirmed by Möller (58). However, further research regarding the types of scars through which *Fomes pini* may enter its host is lacking except for the observations of Boyce (9). By splitting the 16-foot logs cut from 118 Douglas fir trees which were decayed by *Fomes pini*, Boyce observed that 83 per cent of the infections had apparently taken place in branch stubs. The idea is universally held that *Fomes pini* enters its hosts by means of branch stubs or other wounds in the stem as indicated by Abbott (3), Atkinson (7), Eriksson (26) and Hole (42). Evidence that infection may also occur through root grafts has been produced by Khan (44) and Hole (42), but Hole further showed that this method of infection, though possible, was of little consequence. The importance of wind checks as courts of infection in spruce has been stressed by Havelik (39) and there have been observations of decay which followed the pruning of green branches of spruce (2) and larch (1). Weir (80) has shown that blazes in non-resinous trees are closely related to decay and the production of sporophores.

The paper by Cline and Fletcher (17) on the pruning of eastern white pine, *Pinus strobus* L., serves to emphasize the need of specific knowledge as to the exact conditions under which *Fomes pini* infects white pine.

Surveys (9, 81) have shown that large proportions of old stands of Douglas fir and western white pine are destroyed by this organism. In the east, no accurate surveys have been undertaken; however, estimates of the cull produced by *Fomes pini* in eastern white pine stands range from 10 to 50 per cent.

In 1928, the author was interested in making a brief survey of the amount of decay in a pulp-wood cutting of second-growth red spruce. The first cutting of the softwood timber was made approximately 40 years ago. Particular attention was given to the prevalence of *Fomes pini* rot. Sample strips, covering a total area of 15 acres, were located on sites which were classified as the spruce flat and spruce slope variants of Red Spruce Type

Fig. 1. An apparently sound tree, *Picea rubra Link*, the heartwood of which was completely decayed by *Fomes pini*.

18[1]. The inspection and measurement of all the trees and logs (Figs. 1 and 2) which were left in the woods after skidding revealed that on the spruce flats, 10.36 per cent of the total softwood stand had been decayed by *Fomes pini*. Since this kind of decay was confined to red spruce and this species made up about one-half of the coniferous stand, the figure, 10.36 per cent, would indicate that approximately one-fifth of the spruce timber was culled because of the decay produced by this one organism. On the spruce slopes, the damage produced by this fungus was only 2.53 per cent of the total softwood stand. Here, however, other decay fungi were present which were not found on the

Fig. 2. Logs of red spruce abandoned on the skidway because of incipient decay produced by *Fomes pini*.

spruce flat. These fungi had destroyed an additional 2.06 per cent of the softwood timber.

Although these figures may not be considered as accurate estimates of cull in New York State, they were taken in the typical red spruce type and serve to emphasize the economic importance of *Fomes pini* as a cull-producing organism.

Any comprehensive management plan for the production of coniferous timber in the northeastern United States must include effective methods for controlling the organisms of decay. It is essential to have more information concerning the life history of

[1] Type 18 Red Spruce, in Forest Cover Types of the Eastern United States, Journal of Forestry, Volume XXX, No. 4, 1932.

Fomes pini in order to advocate a change in silvicultural methods affecting susceptible species and for the development of control measures. It was the object of this investigation to present certain fundamental data which may be useful for these purposes.

DESCRIPTION OF SPOROPHORE

Although the name, *Trametes pini* (Thore) Fr., has been long established and is still in common usage, the name *Fomes pini*, proposed by Lloyd (47) and used by Overholts (65), Shope (74), and Wolf (83) seems more logical. The tubes are stratified, as Lloyd emphasizes. The sporophores are perennial, or potentially so, and according to Neger (64) may become 50 years old. They continue to grow as long as their substrata remain suitable for the vegetative development of the fungus. Therefore, this plant will be referred to throughout this paper as *Fomes pini*.

The following description is essentially the same as that written by Mr. J. L. Lowe[2]:

> Pileus annual or perennial, sessile or effused-reflexed, sometimes resupinate, thin and conchate, often ungulate, 0–15 × 1–20 × 0.3–15 cm.: surface at first yellowish-brown to reddish-brown with elevated zones of appressed tomentum, becoming grayish-black or brownish-black toward the base, or, in the ungulate form, becoming blackish, glabrous, cracking and becoming rough; margin obtuse to acute, sterile or fertile below; context yellowish-brown to reddish-brown, woody, 1–5 mm. thick, the hyphae rarely branched, rather thick-walled, 3–5 μ in diameter; tubes concolorous or lighter, the walls whitish incrusted, in one layer or indistinctly stratified, 2–6 mm. long each season, mouths yellowish-brown to reddish-brown, angular to sinuous or daedaloid, usually 3–4 per mm., or, in the ungulate form, 1–3 per mm., the edges thin, entire; setae abundant, 8–12 μ in diameter, projecting up to 30 μ; basidia 4–5 μ in diameter; spores hyaline to brown, smooth, subglobose to globose, 4–5 μ.

Varieties based on the annual form of *Fomes pini* are not recognized. In this respect, agreement is made with the treatment of the species given by Shope (74). Year old specimens are often found in New York State on fallen timber of low resin content such as spruce. The author felled several living red spruce trees bearing perennial fruiting bodies, and, after 1 year found fresh sporophores of the annual form upon them (Fig. 3). At the end of the second year, a majority of these had died. One sporophore remained alive for 3 years. The author has counted

[2] Lowe, J. L. The Polyporaceae of New York State (Pileate Species) N. Y. S. Coll. Forestry Tech. Publ. 41. 1934.

as many as 8 layers of tubes in sporophores produced upon fallen spruce timber. The numerous short-lived sporophores which occur on fallen timber are partly responsible for the tendency to retain the old generic name, Trametes, for the fungus, and also for the placement of the annual form in a separate variety as Overholts (65) has done. Retention of a separate status for the annual form does not seem advisable since it may be produced by mycelium within the same tree which produced the perennial form.

In spite of its great variation of form and its world-wide distribution, *Fomes pini* has been described under relatively few names. Murrill (85) lists the following synonyms:

Boletus Pini Thore, Chlor. Land. 487. 1803. —Brot. Fl. Lusit. 2:468. 1804.

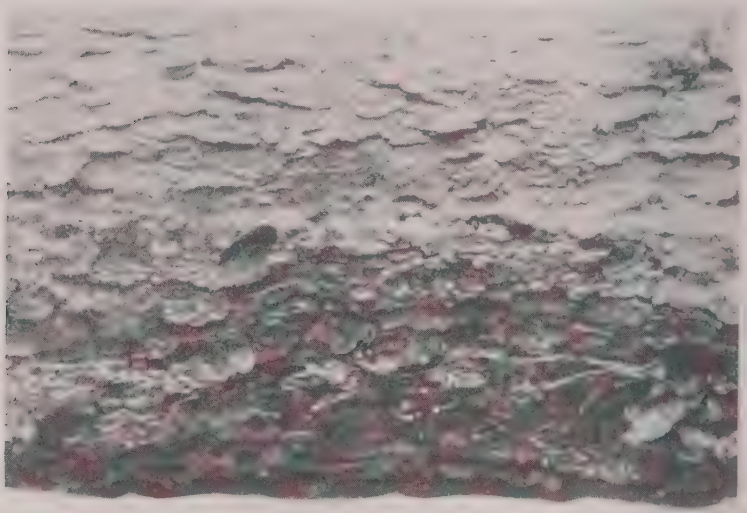

Fig. 3. A decayed red spruce log which was felled while alive and remained on the ground for one year. Young sporophores of *Fomes pini* may be seen growing from the bark.

Daedalea Pini Fries, Syst. Myc. 1:336. 1821. —Linnaea 5:514. 1830.
Polyporus Pini Pers., Myc. Eur. 2:83. 1825.
Trametes Pini Fries, Epicr. Myc. 489. 1838.
Fomes Abietis Karst., Bidr. Finl. Nat. Folk 37:242. 1882.
Polyporus piceinus Peck, Ann. Rep. New York State Mus. 42:25. 1889.
Trametes Pini Abietis Karst., Finl. Basidsv. 336. 1889.
?Trametes gausapata Berk. & Rav., Grevillea 19 :102. 1891.

To this list may be added:

Ochroporus Pini Schrot., Kr. Fl. Schles. 1 p. 487.

Polystictus piceinus (Peck) Sacc., Syll. Fung. 9:187. 1891.

*Poroda*edalea *Pini* (Thore) Murr., Bull. Torr. Bot. Club 32:367. 1905.

Phellinus Pini (Thore) Ames, Ann. Myc. 11:246. 1913.

Xanthochrous pini (Brot.) Pat., Hymen. d. France, page 632. 1928.

Xanthochrous abietis (Karst.) B. and G., Hymen. d. France, page 633. 1928.

Some confusion as to the identity of this fungus has existed among pathologists, not only because of the variations of the fruiting bodies but also because of the different types of decay which are commonly associated with the different forms. For example, a small perennial form of sporophore, common on *Pinus strobus* L., is associated with an evenly distributed reddening of the heartwood and with the formation of a few small, elongated, white pockets in advance decay. This condition of pine wood is known as red rot (Fig. 19). On *Picea rubra* Link, annual sporophores (Figs. 4 and 5) are usually found associated with a honeycombed appearance of the heartwood caused by very numerous white pockets (Fig. 20), similar to those which are found to a lesser extent in pine. Such an area is surrounded with a narrow reddened zone where the decay is in an incipient stage. This decay is called pocket rot and is as familiar a sight in spruce as the red rot is in white pine. On *Pinus ponderosa* Lawson, *Fomes pini* appears as a large perennial conk (Fig. 6) associated with some discoloration and a decay which tends to follow certain annual rings. This results in the complete disintegration of roughly concentric cylinders of wood with intervening sound areas. This condition, known as ring scale (Fig. 21), is far different in appearance from either of the 2 types of decay mentioned above. A culture study of *Fomes pini* on wood blocks supported the contention that the 3 forms of decay, i. e., red rot, pocket rot, ring scale, are caused by the same fungus.

DISTRIBUTION

Geographical

Fomes pini may be found throughout the temperate zone of the northern hemisphere wherever there are coniferous forests. In this country, it has been reported from Alabama, Arkansas, California, Colorado, Florida, Georgia, Idaho, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Texas,

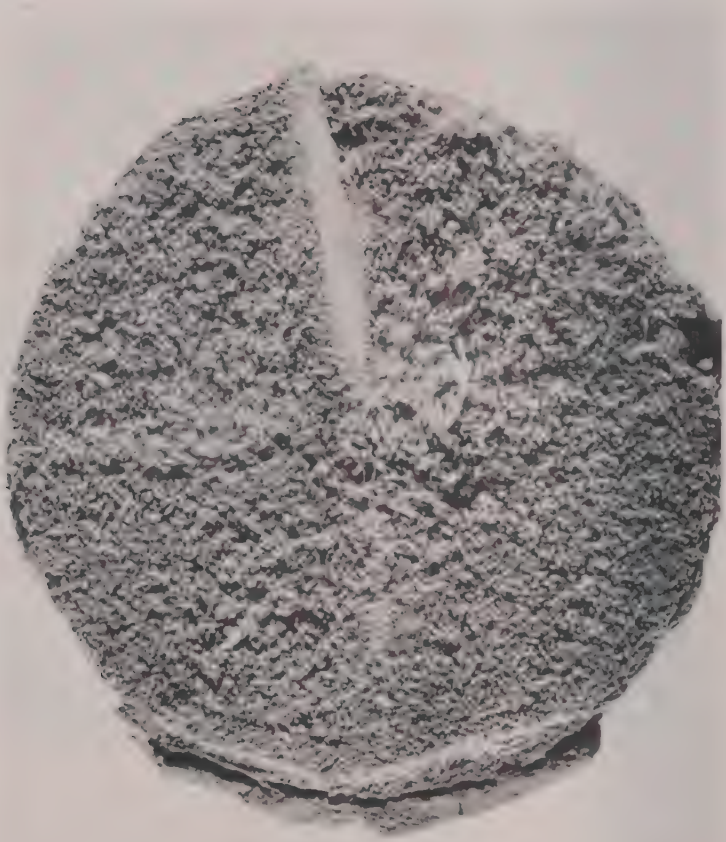

Fig. 4. Transverse section of log, *Picea rubra* Link, with pocket rot. A resupinate sporophore of *Fomes pini* is shown on the lower surface. A sound resin-filled knot penetrates the decayed wood. x ½.

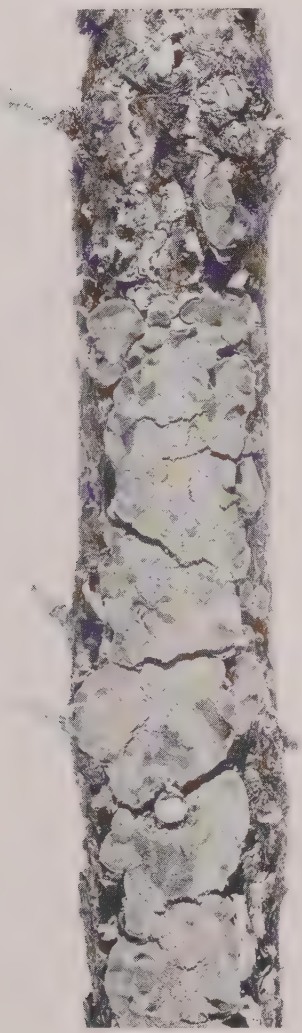

Fig. 5. Sporophore of *Fomes pini* (Thore) Lloyd collected from *Picea mariana* (Miller) Britton, Sterns and Poggenberg. x ½.

Vermont, Washington, West Virginia, Wisconsin, Wyoming, and the District of Columbia. *Fomes pini* is also found in the 2 territories of Alaska and the Philippines and has been reported from Austria, Bavaria, Bohemia, Canada (British Columbia, Ontario, and Quebec), Denmark, France, Germany, Hungary, India (Kashmir and Punjab), Italy, Japan, Moravia, Holland (20), Nova Scotia (27), Portugal, Russia, Siberia, Spain, Sweden, Switzerland, and the West Indies.

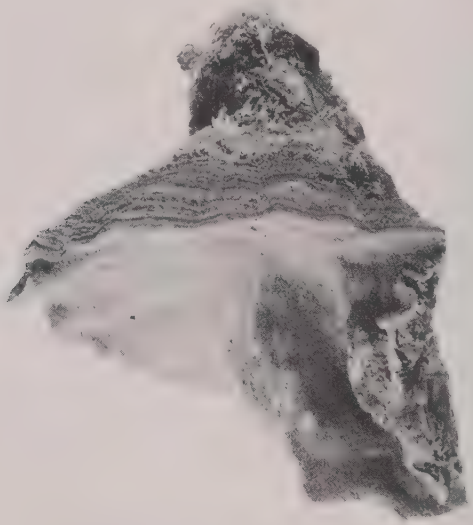

Fig. 6. Sporophore of *Fomes pini* (Thore) Lloyd collected from *Pseudotsuga taxifolia* (LaMarch) Britton. x ½.

Hosts

Fomes pini is found almost exclusively on the conifers. There are only 3 reports of its occurrence on deciduous hosts, i. e., on birch by Weir (79), on maple by Spaulding[2], and on Crataegus by Shope (74). The following host list includes 53 species. It has been compiled from the references cited and from lists of the collections in the Herbarium of the United States Department of Agriculture, Bureau of Plant Industry, the Lloyd Herbarium, the Missouri Botanical Garden, and the New York State College of Forestry.

This list is not considered complete either as to host or locality but it includes a majority of the host trees which have been reported.

[2] Collection in Herbarium, U. S. Department of Agriculture, Bureau of Plant Industry, Washington, D. C.

TABLE 1. *Host list for Fomes pini*

	Host	Locality	Name of Collector
1.	*Abies alba*[4]	Germany	Hartig (78), Hofmann (78)
2.	*A. amabilis*	United States	Boyce (13)
	"	" " Oregon	Weir
3.	*A. balsamea*	United States	von Schrenk (73)
	"	" " New York	Murrill
	" (dead)	" " "	Spaulding
	"	Canada, Quebec	McCallum (55)
4.	*A. concolor*	United States	Boyce (13), Meinecke (57)
	"	" " Oregon	Weir
5.	*A. grandis*	United States, Montana	Weir
6.	*A. lasiocarpa*	United States	Hedgcock (40)
	"	" " Idaho	Stillinger, Weir
	"	" " Montana	Weir
7.	*A. magnifica*	United States	Boyce (13)
8.	*A. magnifica* var. *shastensis*	United States	Boyce (13)
9.	*A. nobilis*	United States	Hedgcock (40)
10.	Acer species	United States, Vermont	Spaulding
11.	*Betula papyrifera* var. *occidentalis*	United States, Idaho	Weir (79), Shattuck
12.	*Chamaecyparis lawsoniana*	United States	Boyce (11)
	"	" " Oregon	Weir
13.	*C. nootkatensis*	Alaska	Drake
14.	*Cedrus libani* var. *deodar*	India, Kashmir	Singh (75), Suri (77)
15.	Crataegus species	United States, Colorado	Shope (74)
16.	*Larix decidua*	Germany	Hartig (78)
17.	*L. laricina*	United States, Michigan	Bonar
	" (log)[5]	" " New York	Percival
	"	" " Minnesota	Weir
	" (living)	" " Wisconsin	Neuman
	"	Canada, Ontario	Dearness
18.	*L. lyallii*	United States, Montana	Weir
19.	*L. occidentalis*	United States	Mayr (78)
	"	" " Idaho	Weir, Hubert
	" (log)	" " Washington	Rhoads
	"	" " Montana	Hubert, Weir
20.	*Libocedrus decurrens*	United States	Boyce (13)
21.	*Picea Abies*	Germany	Hartig (78)
	"	"	Krieger, Weir
	"	Scandinavia	Romell
	"	Austria	Fromme
22.	*P. ajanensis*	Japan	Mayr (78)
23.	*Picea breweriana*	United States, Oregon	Pernot
24.	*P. engelmannii*	United States, Idaho	Boyce, Hedgcock, Weir
	"	" " Montana	Weir
	" (dead)	" " Colorado	Bethel & Johnston
	"	Canada, Br. Columbia	Weir, Macoun
25.	*P. glauca*	United States	von Schrenk (73)
	" (living, log)	" " New York	Percival

	Host	Locality	Name of Collector
26.	*P. mariana*	United States	Hedgcock (40)
	"	" " Minnesota	Hubert
	"	" " Michigan	Pennington
	" (log)	" " New York	Pennington, Percival
27.	*P. Omorika*	Germany	Geschwind (33)
28.	*P. rubra*	United States	Atkinson (78)
	" (living)	" " New York	Percival
	" (dead, log)	" " New York	Percival
	"	" " N. Carolina	Korstian
	"	" " Vermont	Burt
29.	*P. sitchensis*	United States	Boyce (11), Mayr (78)
	"	" " Washington	Meinecke
30.	*Pinus albicaulis*	United States	Weir
31.	*P. banksiana*	United States, Michigan	Weir
32.	*P. clausa*	United States, Florida	Hedgcock
33.	*P. Cembra*	Germany	von Tubeuf (78)
34.	*P. contorta*	United States	Boyce (13), Mayr (78)
	"	United States, Washington	Weir
	"	" " Idaho	Hubert
	"	" " Montana	Weir
35.	*P. echinata*	United States, Missouri	von Schrenk
	"	" " W. Virginia	Bonar
	"	" " Arkansas	Keifer
36.	*P. edulis*	United States	Hedgcock (40)
	"	" " Colorado	Bethel & Hunt
37.	*P. excelsa*	India	Hole (42), Mayes
	"	" Punjab	Trevor
38.	*P. flexilis*	United States	Hedgcock (40)
	"	" " Montana	Weir
39.	*P. halepensis*	France	Durand (25), Arnaud (6)
40.	*P. lambertiana*	United States	Boyce (13)
	"	" " California	Hedgcock
41.	*P. maritima*	France	Dufrenoy (23)
	"	Portugal	Torrend
	"	Italy	Fiori
42.	*P. Mugo*	Germany	von Tubeuf (78)
43.	*Pinus monticola*	United States	Martin (51)
	"	" " Idaho	Hubert, Weir
	"	" " Montana	Weir
44.	*P. palustris*	United States, Texas	Spaulding
	"	" " New York	Dudley (22)
45.	*P. ponderosa* (log)	United States	Boyce (12), Long (49)
	"	" " Idaho	Weir
	"	" " Montana	Hedgcock
46.	*P. resinosa*	United States	Boyce, Hedgcock (40)
	"	" " Minnesota	Weir
47.	*P. rigida*	United States, New Jersey	Ellis
	"	" " Kentucky	Deschamps
	"	" "	Boyce (13)
48.	*P. sylvestris*	Germany	Hartig (78), Sydow
	"	Bavaria	Weir
	"	Russia	Younitsky (84), Newodowski

	Host	Locality	Name of Collector
	"	Bohemia	Bubak
	"	Sweden	Lloyd
	"	Hungary	.....
	"	United States, Michigan...	Webster
49.	*P. strobiformis*	United States	Boyce (13), Hedgcock (40)
50.	*P. strobus*	United States	Mayr(78), von Schrenk(78)
	" (living, log)	" " New York..	Percival
	"	" " N. Carolina.	Graves (34)
51.	*P. taeda*	United States	Boyce (13), Hedgcock (40)
52.	*P. virginiana*	United States, Washington, D. C.....	Hedgcock
	"	" " Maryland..	Hedgcock, Rhoads, Stevenson
	"	" " Georgia....	Graves (35)
	"	" "	Boyce (13)
53.	*Pseudotsuga taxifolia.*	United States, Wyoming...	von Schrenk
	"	" " Idaho.....	Boyce (11), Rhoads, Schmitz (52)
	"	" " Oregon....	Weir, Owens, Griffith
	"	" " Washington	Weir, Hotson
	"	" " California..	Hubert, Parks
	"	" " Montana...	Weir
	"	Canada, Br. Columbia....	Lachmund, Macoun
54.	*Taxus baccata*	Germany	von Tubeuf (78)
55.	*Thuja plicata*	United States, Idaho.....	Weir
	"	" " Montana...	Weir
56.	*Tsuga canadensis*	United States	von Schrenk (78)
57.	*T. heterophylla*	United States, Idaho.....	Weir
	"	" "	Boyce (13), Hedgcock (40)
	"	" " Oregon.....	Gribble
	"	" " Washington	Weir
	"	Alaska	Weir
58.	*T. mertensiana*	United States, Washington	Hedgcock (40)
	"	" " Oregon.....	Weir
	"	" " Idaho.....	Weir

[4] Names of native trees throughout this paper are given according to the "Check List of the Forest Trees of the United States, Their Names and Ranges," by George B. Sudworth, Washington, 1927. All others are given according to the "Manual of Cultivated Plants," by L. H. Bailey, New York, 1925.

[5] A description of the host is given where known as follows: (living) indicates that the sporophore was found on the living tree; (dead) indicates that the host was dead but still standing; (log) indicates that the collection was made from the fallen tree either sawed into sections as in logging or whole.

OCCURRENCE

Fomes pini is generally considered to be a trunk-rot fungus which occurs, as stated by Lloyd (47), relatively high in the bole of the tree. This opinion has been confirmed by every investigator who has reported on this subject. It has, however, also been found by Weir and Hubert (82) to cause a typical butt rot on *Pinus monticola* D. Don. The presence of the fungus in the roots has been reported by Hedgcock (40), Hole (42) and Khan (44). On spruce in New York State, the author has found that it extends into the roots as well as into the branches.

Thirty trees of *Picea rubra* Link infected with *Fomes pini* were felled and cut into sections, 5 feet in length. The wood was classified as either apparently sound or in 1 of 2 stages of decay. It was considered to be in a condition of incipient decay when abnormally reddened or in a condition of advanced decay when characterized by the presence of white pockets, sufficient in number to give it a honey-combed appearance. Advanced decay was found to be rather evenly distributed throughout the heartwood, irrespective of the point of infection. Of the 30 trees dissected, 2 were examined below the ground line. The roots of these 2 for a distance of 5 feet contained the typical pocket rot caused by *Fomes pini*.

The contours of the various stages of decay in one representative tree are outlined to scale in figure 7. The interesting feature of the decayed trunks was the constant occurrence of at least a thin cylinder of apparently sound sapwood just inside the cambium, regardless of the extent of decay in the heartwood. The narrowest of these cylinders of apparently sound wood included 11 annual rings, while several showed 12 to 15 rings of yearly growth. In no case did the decay extend into the living cambium, as shown subsequently in this paper. This condition seemed to point to a saprophytic relationship between *Fomes pini* and *Picea rubra*.

Hartig (37) found that the hyphae of this fungus do not enter the sapwood, hence, the living cells, of *Pinus sylvestris* L. and Quinier (68) has recently stated that it is unable to attack the sapwood of pine because of the abundant resin flow. Von Schrenk (73) stated that the mycelium of *Fomes pini* grew in both heartwood and sapwood of spruce, hemlock, fir, and larch but that it occurs only in the heartwood of pine. Abbott (3) disagreed with this statement and indicated that this fungus may grow also through sapwood, cambium and bark of a living pine. Hedgcock (40) stated that "in some instances trees are killed outright", and Shope (74) classified *Fomes pini* as a parasite.

A parasite may be considered as an organism which obtains nourishment from living cells. All of Hartig's data were taken from the one species, *Pinus sylvestris* L., the wood of which has

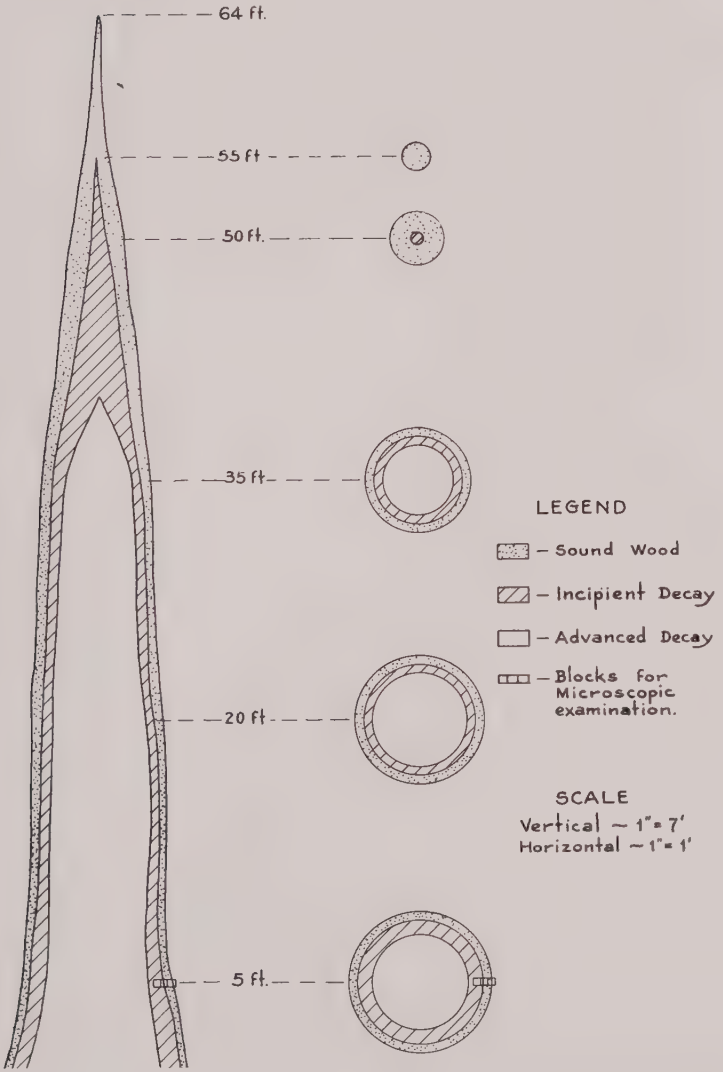

Fig. 7. Diagram of longitudinal and transverse sections of the trunk of a red spruce decayed by *Fomes pini*. Bark is omitted.

a comparatively high resin content. Hartig placed considerable emphasis on the presence of the resin in the living tissue as an inhibiting influence on the growth of *Fomes pini* mycelium. Therefore, the condition of obligate saprophytism which he found to exist between *Fomes pini* and *Pinus sylvestris* might not hold true for a wood of such low resin content as *Picea rubra* Link, as von Schrenk's statement would indicate.

In order to gain information regarding this point, microscopic examinations were made of the sapwood and adjoining heartwood. Consecutive blocks, located as shown in figure 7, were cut from the wood of each of 6 dissected trees. The blocks were placed in formalin-acetic-alcohol[6] immediately after they were taken from the tree. They were then imbedded in celloidin according to Lodewick's (48) schedule, and sections were cut to 15 microns. The details of hyphal penetration were brought out by 3 combination stains, i. e., Haidenhain's haematoxylin and safranin according to Chamberlain's (16) methods, Boyce's (8) malachite-green and acid fuchsin, and Durand's (24) haematoxylin and eosin. The best results were obtained with Haidenhain's haematoxylin and safranin which stained the hyphae, middle lamellae, and protoplasmic cell contents of the wood various shades of blue in sharp contrast to the secondary walls which became red.

The fungous hyphae were observed in the heartwood in all of the 6 trees mentioned above. In no case, however, were they found in the living cells of the sapwood. Further, it was noted that in the wood examined, they failed to penetrate the annual rings which contained living parenchymatous tissue. The presence of nuclei was the criterion used to distinguish live cells. In the particular instance where the hyphae most closely approached the living tissue, nuclei were found to be present in the parenchyma of the ninth annual ring (inward from the cambium), whereas the hyphae were found in the eleventh ring.

The sapwood of *Picea rubra* is not distinctly separated from the heartwood on the basis of color. The basis for the separation in this work was the presence or absence of living parenchyma. If this is used as the criterion, it may be said that the mycelium of *Fomes pini* did not enter the sapwood of *Picea rubra* in any of the trees studied, thus agreeing with Hartig's findings in *Pinus sylvestris*. This further indicated that *Fomes pini* enters red spruce only as a saprophyte.

The saprophytic nature of this organism has been questioned, partly, because its normal habitat seems to be that of the living tree. Von Schrenk (72) expressed the opinion that the growth of *Fomes pini* stops when the tree is felled, and that fruiting bodies are not produced on fallen timber. This is clearly incorrect, how-

[6] Glacial acetic acid, 5 cc.
Commercial formalin, 5 cc.
Alcohol, 70% 90 cc.

ever, as the fruiting bodies of this fungus, in New York State, are commonly produced on fallen timber; in fact, the production of sporophores on spruce becomes pronounced only after the trees have fallen.

Decayed spruce logs which have been abandoned after a logging operation, such as those shown in figure 2, bear an abundance of small, short-lived sporophores.

On pine, the fruiting bodies are rarely produced on felled timber. Peck (66) inserted a note into his 1905 report to the effect that *Fomes pini* was found near Albia, New York, growing on pine ties of the electric railroad, a rare occurrence. Boyce (10) found this fungus in felled *Pinus ponderosa* Lawson but noted that it was growing very slowly if at all. Spaulding (76) noted the absence of *Fomes pini* in white pine slash in New England. It is safe to state that living sporophores of this organism are infrequent on fallen pine but of common occurrence on fallen timber of low resin content such as red spruce.

SPORULATION

Two principal points were considered in regard to the sporulation of *Fomes pini*, namely, the period of spore cast and the meteorological stimuli which influence sporulation.

Periods of Sporulation

Sporulation records were made from spore casts on ordinary glass slides placed in spore traps. The traps were constructed from cylindrical tin cans, 15 cm. long by 11 cm. wide. In order to lessen the air currents within the trap, each can was carefully fitted about a sporophore growing on the side of a log. The spores were caught on glass slides 7.5 cm. x 2.5 cm., which were always supported in exactly the same position at a distance of 1 cm. from the pore surface. Spores were collected in traps of this kind from 11 different fruiting-bodies situated as shown in table 2.

TABLE 2. *Placement of spore traps*

Locality	Host	Number of traps
Clearwater, N. Y.	*Picea rubra*	2
Pleasant Lake, N. Y.	*Larix laricina*	1
Pleasant Lake, N. Y.	*Picea mariana*	1
Syracuse, N. Y.	*Picea rubra*	2
Jamesville, N. Y.	*Picea rubra*	2
Jamesville, N. Y.	*Picea glauca*	3

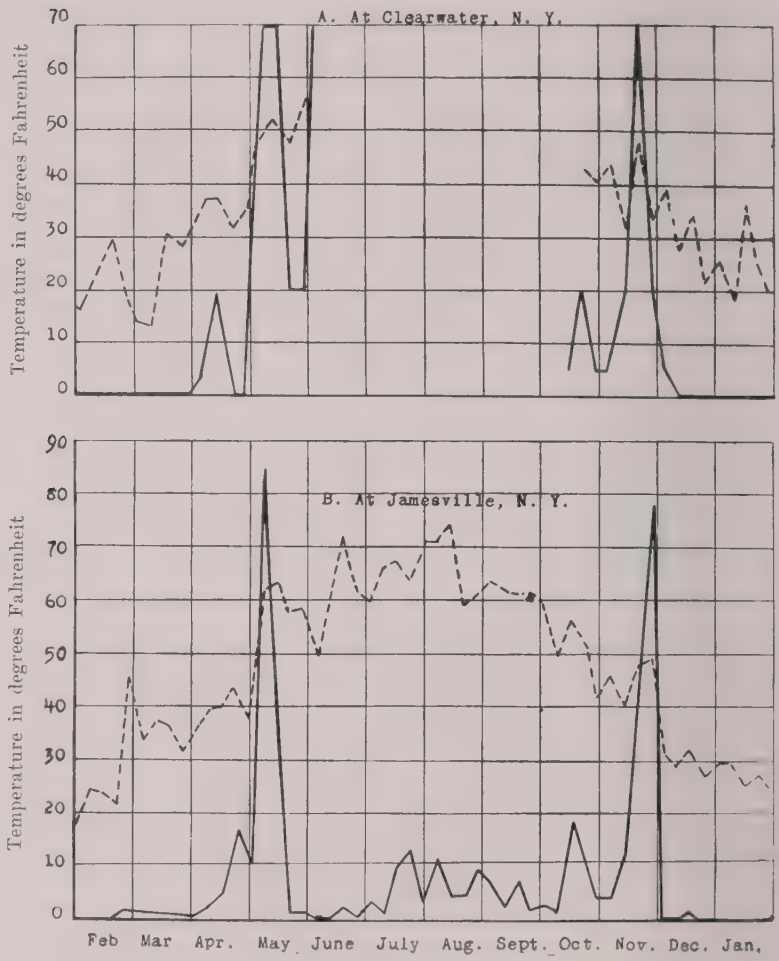

Fig. 8. Sporulation of *Fomes pini* computed on a weekly basis to show seasonal periods of high spore cast. 1930–31.

The slides which were placed in the traps on *Picea rubra* logs at Clearwater, New York, were collected once each week from October 14, 1927 to June 2, 1928. The volume of sporulation was estimated and recorded as heavy, medium, light, and negative. Temperature readings were taken at 5 A. M. and 2 P. M. every day from a standardized thermometer placed near the traps, and averages were compiled on a weekly basis.

The following year a more intensive study, over a full 12 months period, was made at Jamesville, New York, a station which is roughly 100 miles south of Clearwater. Here, sporulation records were made from slides placed in 5 traps, 2 on *Picea rubra* and 3 on *P. glauca* logs. For this study, the volume of sporulation was derived by counting the spores which fell on unit areas. Each unit area measured 0.04 sq. mm. and was layed out with a Sedgwick-Rafter square-ruled eyepiece. Forty-five of these were counted on each slide. The areas were carefully located by means of a mechanical stage, in 3 rows running lengthwise of the slide. The middle row was located in the center of the slide while the other 2 rows were 2 mm. inside the upper and lower margins. These areas were located with such precision that the spores which were counted came from approximately the same pores each week. In this manner, the spores which fell on a total area of 1.8 sq. mm. on each slide were accurately determined.

The spore counts, made every week on each of 5 slides, yielded similar results. These were averaged and the resulting figures, which represent the average number of spores cast during a week on an area of 1.8 sq. mm., were used as an index of sporulation.

At Jamesville, New York, the temperatures were recorded on a Fries hygrothermograph. The instrument was placed in the usual hygrothermograph shelter within 10 feet of the spore traps and on the same level with them. Weekly averages were obtained from the hygrothermograph records and used as a temperature index. The sporulation index and temperature index figures compiled from the studies carried out at Jamesville, New York are recorded in table 3. These are graphically compared with the observations at Clearwater, New York, in figure 8.

TABLE 3. *Sporulation and temperature indices compiled from studies at Jamesville, New York*

Week ending	Temperature average per week in degrees Fahrenheit [7]	Sporulation index. Average spore-cast from 5 sporophores [8]
1930		
Feb. 3	24.9	0
" 10	24.1	0
" 17	22.0	0
" 24	47.0	10
Mar. 3	35.3	3
" 10	38.2	1
" 17	37.7	3
" 24	32.8	42
" 31	37.7	7
April 7	40.4	32
" 14	40.9	82
" 21	45.0	267
" 28	38.6	157
May 5	62.9	1296
" 12	65.0	478
" 19	59.3	19
" 26	59.9	22
June 2	50.5	11
" 9	62.1	7
" 16	73.0	40
" 23	62.9	13
" 30	61.0	65
July 7	67.3	14
" 14	68.5	156
" 21	64.7	198
" 28	72.7	49
Aug. 4	72.5	183
" 11	76.0	67
" 18	60.3	73
" 25	62.1	145
Sept. 1	65.7	108
" 8	63.3	31
" 15	62.3	117
" 22	62.3	20
" 29	60.0	70
Oct. 6	49.8	27
" 13	57.4	286
" 20	52.0	180
" 27	42.1	62
Nov. 3	46.7	55
" 10	39.9	206
" 17	48.1	581
" 24	49.8	1197
Dec. 1	31.5	7
" 8	29.6	1
" 15	31.7	24
" 22	27.0	1
" 29	29.2	0

Week ending	Temperature average per week in degrees Fahrenheit [7]	Sporulation index. Average spore-cast from 5 sporophores [8]
1931		
Jan. 5	29.1	0
" 12	25.5	0
" 19	27.0	1
" 26	24.5	0

[7] Temperature average computed from bihourly records taken from Fries hygrothermograph.
[8] Sporulation index computed from weekly spore casts from 5 sporophores. The figures represent the average number of spores cast during 1 week upon 1.8 sq. mm. of surface of glass slide.

It is of interest to note that there were 2 brief periods of heavy sporulation, one in the spring, the other in the fall, and that these periods coincided with a rise in the average weekly temperature. It is of further interest to notice that at least a few spores were cast at all times of the year except when the average weekly temperature dropped below the freezing point of water. No correlation could be found between the number of spores cast and any particular percentages of relative humidity. It is noteworthy, however, that periods of high sporulation are accompanied by widely fluctuating relative humidities, as shown in figure 10.

Meteorological Stimuli and Effect on Daily Sporulation

It was noted that heavy sporulation was coincident with rises in the average weekly temperatures following cool periods. In order to gain more accurate data regarding the fluctuations of temperature which accompanied changes in sporulation, records were made of the daily spore casts from 2 sporophores in a manner similar to that previously described for the weekly records. Counts of the spore casts were made every day from January 3, 1930 to May 12, 1930. These spore counts furnished the basis for a sporulation index which was correlated with hygrothermograph records of temperature and relative humidities.

During the period of winter dormancy, a rise in temperature above freezing for a few hours did not induce sporulation. The longest period of this kind occurred on February 12 and 13. As shown in figure 9, the temperature remained above freezing for 32 hours, without the appearance of any spores in the traps.

Very light sporulation began on February 20 after 3 days during which the temperature was above freezing. As shown in figure 9, a light spore cast occurred every day for 8 days; on

February 23, a maximum of 23 spores was found, after which there were fewer spores each day until sporulation ceased on February 28. These counts seem very small when they are compared with the large numbers which were cast later in the season. Nevertheless it is significant that sporulation began after 3 days of warm temperatures and that it did not stop completely until after 2 days of average daily temperatures below 32°F.

During the following 4 weeks that is, until March 27, 1930, there were 3 periods of light sporulation all of which were shorter than the one just described; in other respects they were similar. On March 27, 1930, sporulation began and continued through the third week of December in spite of brief drops in temperature below 32° F. during the spring and fall.

Although there was at least a small amount of sporulation whenever the average weekly temperature was above freezing, no great abundance of spores was produced until more exacting conditions occurred. When heavy spore casts occurred, they were preceded by cool weather, with light sporulation, and followed by a rise in temperature. The details of these changes can be followed in figure 10. For several days prior to April 26, the weather had been quite uniformly cool, but beginning with that date, there were wide fluctuations of temperature which reached well above 50° F. The humidity fluctuated even more widely than the temperature. During this period, the sporulation was very heavy and continued so for nearly 10 days. Near the end of the high sporulation period, the spore casts decreased each day without being preceded by any pronounced changes in weather conditions, until the number of spores approximated those of the cool weather earlier in the year.

Several sporophores were examined at this time (May 19, 1930) and they revealed the presence of bright yellow hyphae growing into the tubes of the hymenophore. This condition seemed to indicate that the protracted period of high temperatures was conducive to vegetative growth. This growth continued until a new layer of tubes was formed. During all of this time spores were cast, although, at times, they were very few in number.

It was impossible to find any close correlation between spore cast and relative humidity. It is apparent that wide fluctuations of relative humidity were accompanied by heavy sporulation. It should be kept in mind, however, that these wide fluctuations in relative humidity are directly associated with wide fluctuations in temperature.

Further investigation into the influence of temperature and humidity upon sporulation was attempted with the aim of discovering whether heavy sporulation coincided with some particular temperature that occurred above 32° F. A clinostat was improvised from a clock upon which a circular platform was mounted

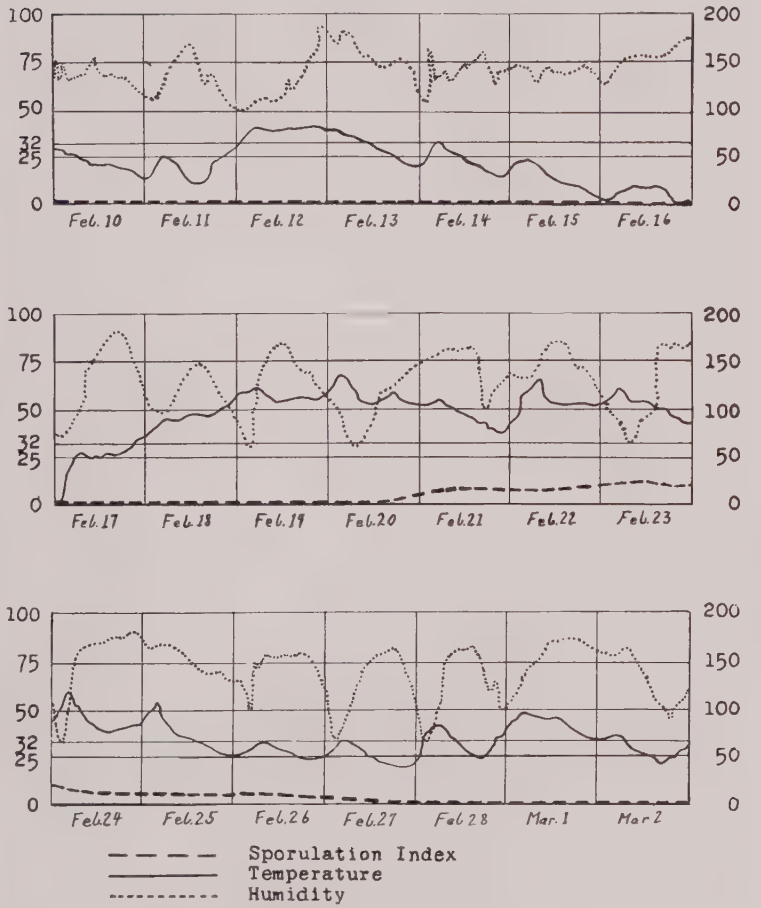

Fig. 9. Sporulation of *Fomes pini* computed on a daily basis to show influence of temperature upon spore cast. 1930.

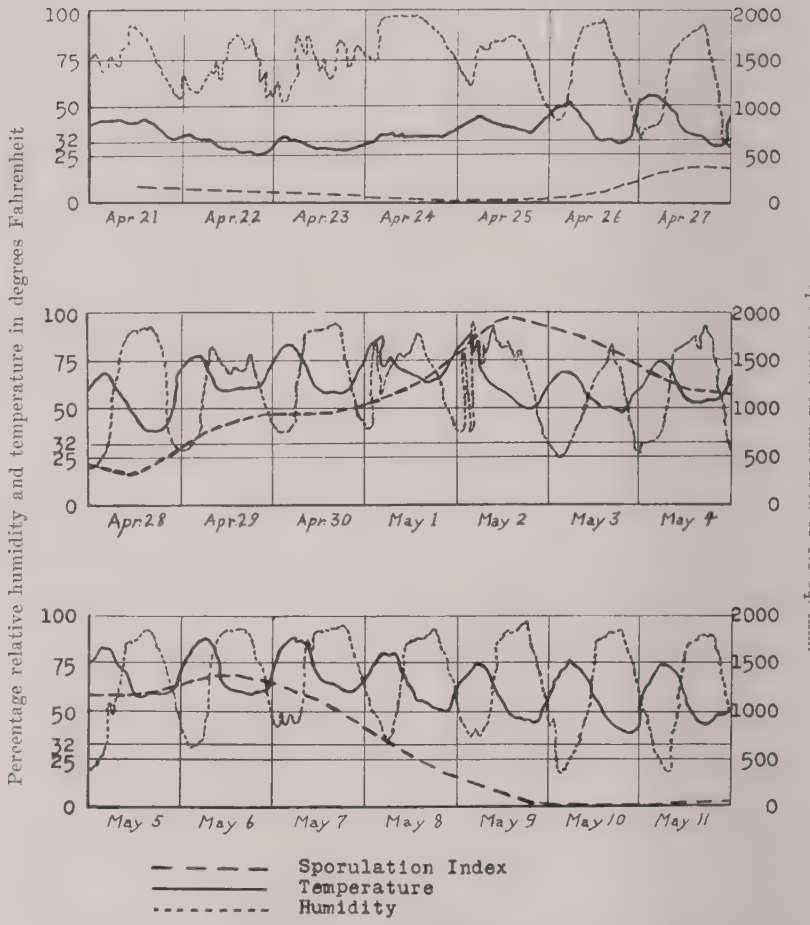

Fig. 10. Sporulation of *Fomes pini* computed on a daily basis to show influence of temperature upon spore cast. 1930.

in such a manner that it revolved once every 12 hours. A glass disk was placed upon the circular platform and held in position by 2 thin rubber bands. The instrument was placed in a tin box through the top of which an aperture was cut and was directly over a section of the glass disk. This opening was shaped like a V, the point of which was carefully located over the center of the clinostat platform. The size of the aperture was such that it exposed exactly one-sixth of the revolving disk. Therefore every point on the disk would be exposed for 2 hours out of every 12. The box, containing the clinostat, was placed beneath a sporophore of *Fomes pini* with the sides of the V-shaped aperture placed directly against the pore surface. This surface was carefully marked so that the box could be removed and again placed in exactly the same position. Every 12 hours, the glass disk was removed and replaced by a new one. The rubber bands which were used to secure the disk were replaced each time to avoid reintroduction of previously cast spores.

For the purpose of obtaining an index of the bihourly sporulation, 6 radii were marked off on the glass disk, spaced 60 degrees apart. Along each radius a primary strip was located, 35 mm. long by 0.2 mm. wide. It required 2 hours for each strip to pass beneath the V-shaped aperture in the tin cover and during this time it received a proportional number of the spores which were cast. In addition to these 6 strips, 2 secondary strips were located at 10 degrees distance on either side of each of the primary ones. The strip located upon a primary radius together with the 2 neighboring strips were examined and the spores counted. These counts were used as a basis for a sporulation index of each two-hour period.

It is evident that the additional strips located at 10 degrees distance from the primary radius must pass under the aperture a short time ahead of or behind the central strip for which the time was reckoned. This projects a slight error into the spore count figures, tending to "level off" the results but not affecting the general contour of the curves based upon them. These curves are represented in figure 11. By using 3 strips instead of 1 as a basis for a sporulation index, the total area examined was increased by 200 per cent. The enlarged area represented in the counts was considered of sufficient advantage to offset the error in time.

In table 4, the number of spores cast during the two-hour periods are compared, first, with the temperature recorded by the hygrothermograph and, second, with the temperature of the context of the sporophore from which the spore cast was being recorded. The latter record was made from readings taken from a standardized thermometer imbedded in the context of the fruiting body. The bihourly sporulation index was plotted directly

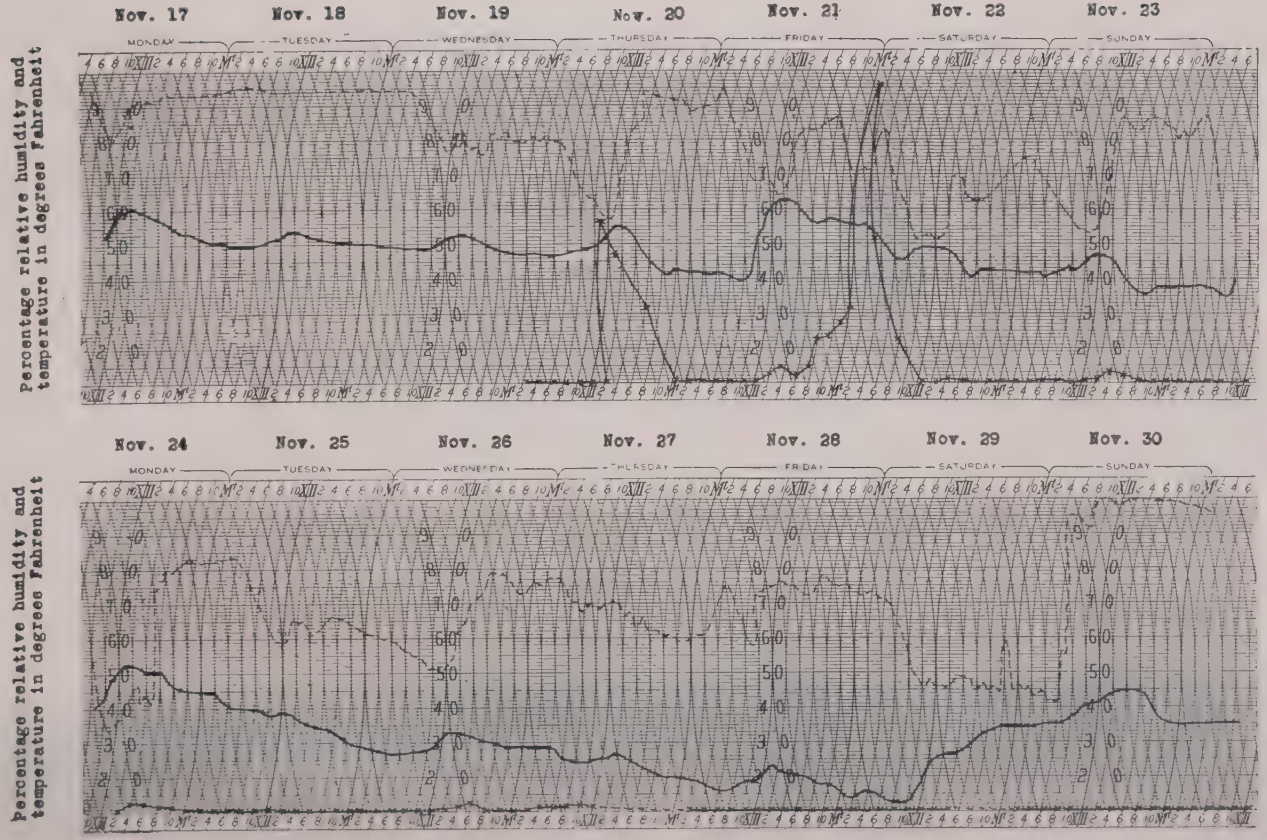

Fig. 11. Sporulation of *Fomes pini* computed on a bihourly basis to show the influence of temperature. Sporulation index plotted directly on hygrothermograph records. Each cross on sporulation index curve indicates one bihourly spore count.

upon the hygrothermograph records from which the temperature figures were obtained for table 4 and the graph is presented in figure 11.

The first 2 days, during which bihourly observations were recorded, occurred on November 20 and 21 at the end of the November period of heavy sporulation as indicated in table 3. On November 20, coincident with a rise in temperature from 47° F. to 54° F. and a drop in the relative humidity of 23 per cent, an abrupt rise in the sporulation occurred. This is shown by a rise in the sporulation index from 36 to 4640. The spore cast continued in large volume for 6 hours and then, simultaneously with a drop in temperature below 50° F., the sporulation index fell from 2161 to 59.

Again on November 21, with a rise in temperature from 40° F. to 62° F. and a drop in the relative humidity of 31 per cent, another period of pronounced sporulation began. This started more slowly than the first but culminated with a sporulation index of 8585. After the maximum sporulation was reached, the spore cast decreased rapidly with the lowering of the temperature. During the next 9 days there were no spectacular rises in sporulation, although there were small increases which were concurrent with slight rises in temperature. On November 25, the temperature went below the freezing point of water and for the ensuing 4 days rose but once to 32° F. and then only for a few hours. Nevertheless, it may be noticed in table 4 that the temperature of the context of the sporophore never went below 31° F. which at one time was 17 degrees above the outside temperature. During all this period, sporulation continued although greatly decreased in amount.

It may be noticed in table 4 that during every rise or fall of temperature as recorded by the hygrothermograph, the decrease or rise in temperature inside of the context of the fruiting body lagged by a few degrees. On November 20, the rise accompanying sporulation was only 7 degrees and inside the sporophore the temperature lagged but 1 degree.

A comparison of the graphs of the temperature and sporulation in figure 11 shows that on November 20, there was but very little lag in the sporulation. It increased almost as quickly as the temperature. On November 21, however, the sporulation lagged several hours behind the rise in temperature. It is possible that this tardy increase of sporulation may be explained by a corresponding lag in the rise of temperature inside the sporophore. Furthermore it seems reasonable to account for sporulation at temperatures below the freezing point of water by the fact that the sporophore does not cool as rapidly as the surrounding air.

Throughout these studies on sporulation of *Fomes pini,* the

TABLE 4. *Bihourly record of sporulation and temperature*

Date	Hour	Sporulation index	Temperature, Degrees Fahrenheit	
			Hygrothermograph	Context of sporophore
Nov. 19	8–10 P.M.	8	48	
	10–12 "	6	47	
Nov. 20	12– 2 A.M.	13	47	
	2– 4 "	8	47	
	4– 6 "	8	47	
	6– 8 "	12	48	47
	8–10 "	36	49	
	10–12 "	4,640	51	
	12– 2 P.M.	3,736	54	
	2– 4 "	2,161	53	
	4– 6 "	59	47	
	6– 8 "	37	42	45
	8–10 "	38	41	
	10–12 "	44	43	
Nov. 21	12– 2 A.M.	37	42	
	2– 4 "	43	41	
	4– 6 "	39	41	
	6– 8 "	31	40	42
	8–10 "	272	46	
	10–12 "	497	55	
	12– 2 P.M.	177	62	
	2– 4 "	464	62	
	4– 6 "	1,231	58	
	6– 8 "	1,328	56	56
	8–10 "	1,737	57	
	10–12 "	2,175	56	
Nov. 22	12– 2 A.M.	8,585	55	
	2– 4 "	4,121	53	
	4– 6 "	1,263	48	
	6– 8 "	19	46	47
	8–10 "	19	48	
	10–12 "	111	49	
	12– 2 P.M.	74	48	
	2– 4 "	17	46	
	4– 6 "	39	41	
	6– 8 "	64	43	42
	8–10 "	50	42	
	10–12 "	23	42	
Nov. 23	12– 2 A.M.	73	42	
	2– 4 "	94	42	
	4– 6 "	61	41	
	6– 8 "	99	43	42
	8–10 "	101	46	
	10–12 "	335	47	
	12– 2 P.M.	233	46	
	2– 4 "	70	43	
	4– 6 "	23	37	
	6– 8 "	49	36	41

TABLE 4. *Bihourly record of sporulation and temperature*—Continued

Date	Hour	Sporulation index	Temperature, Degrees Fahrenheit	
			Hygrothermograph	Context of sporophore
	8–10 "	35	38	
	10–12 "	36	38	
Nov. 24	12– 2 A.M.	40	38	
	2– 4 "	56	37	
	4– 6 "	28	36	
	6– 8 "	59	40	40
	8–10 "	60	43	
	10–12 "	255	48	
	12– 2 P.M.	210	52	
	2– 4 "	173	51	
	4– 6 "	146	51	
	6– 8 "	75	47	47
	8–10 "	51	46	
	10–12 "	27	46	
Nov. 25	12– 2 A.M.	35	45	
	2– 4 "	43	43	
	4– 6 "	45	40	
	6– 8 "	73	40	43
	8–10 "	44	39	
	10–12 "	38	38	
	12– 2 P.M.	31	38	
	2– 4 "	22	36	
	4– 6 "	22	34	
	6– 8 "	18	32	40
	8–10 "	34	29	
	10–12 "	26	28	
Nov. 26	12– 2 A.M.	16	28	
	2– 4 "	29	27	
	4– 6 "	49	26	
	6– 8 "	55	27	37
	8–10 "	66	30	
	10–12 "	112	31	
	12– 2 P.M.	249	32	
	2– 4 "	33	31	
	4– 6 "	40	30	
	6– 8 "	21	29	36
	8–10 "	58	29	
	10–12 "	133	29	
Nov. 27	12– 2 A.M.	129	29	
	2– 4 "	150	27	
	4– 6 "	210	25	
	6– 8 "	140	24	35
	8–10 "	.....	25	
	10 12 "	.....	26	
	12– 2 P.M.	.....	26	
	2– 4 "	.....	23	

TABLE 4. *Bihourly record of sporulation and temperature* — Concluded

Date	Hour	Sporulation index	Temperature, Degrees Fahrenheit	
			Hygrothermograph	Context of sporophore
	4– 6 "	.....	21	
	6– 8 "	.....	20	31
	8–10 "	50	20	
	10–12 "	22	19	
Nov. 28	12– 2 A.M.	43	17	
	2– 4 "	22	16	
	4– 6 "	42	18	
	6– 8 "	56	19	32
	8–10 "	27	21	
	10–12 "	25	22	
	12– 2 P.M.	25	21	
	2– 4 "	9	20	
	4– 6 "	22	18	
	6– 8 "	20	16	
	8–10 "	19	14	
	10–12 "	18	15	
Nov. 29	12– 2 A.M.	21	15	
	2– 4 "	28	13	
	4– 6 "	51	12	
	6– 8 "	41	18	32
	8–10 "	40	22	
	10 12 "	46	25	
	12– 2 P.M.	.....	26	
	2– 4 "	.....	28	
	4– 6 "	.....	30	
	6– 8 "	.....	33	32
	8–10 "	24	34	
	10–12 "	26	35	
Nov. 30	12– 2 A.M.	20	35	
	2– 4 "	30	35	
	4– 6 "	22	35	
	6– 8 "	26	37	36
	8–10 "	30	39	
	10–12 "	38	41	
	12– 2 P.M.	34	43	
	2– 4 "	24	45	
	4– 6 "	34	45	
	6– 8 "	32	41	
	8–10 "	35	36	
	10–12 "	53	35	
Dec. 1	12– 2 A.M.	53	35	
	2– 4 "	50	35	
	4– 6 "	44	35	
	6– 8 "	41	36	37

increase in spore cast concurrent with a rise in temperature has been emphasized several times. It has also been indicated, that these changes were often accompanied by a decrease in relative humidity. However, confirmation of the fact that these concurrent meteorological phenomena actually caused the changes in sporulation, has been lacking. In order that data might be obtained on this subject, fruiting bodies together with their substratum were placed under controlled conditions in an incubator. A section of a trunk of *Picea rubra* Link 20 x 12 inches was used upon which a living sporophore was growing. A relatively constant moisture content was maintained in the sporophore and substratum by spraying water from an atomizer upon the cut end of the log at regular intervals. Bihourly sporulation counts correlated with hygrothermograph records, were made in a manner similar to those previously described.

Within the incubator a temperature of 75° F. and a relative humidity of 95 per cent was maintained for 4 days. During this time, sporulation ceased and vegetative growth started as indicated by the appearance of yellow hyphae in some of the tubes. While keeping the relative humidity constantly above 90 per cent, the temperature was lowered and maintained at 49° F. for 10 days, after which it was raised slowly to 68° F. During the 10 day period at 49° F., there was no noticeable increase in vegetative growth. When the temperature rose to 68° F., light sporulation began and continued for 18 hours, after which the temperature was again dropped to 49° F. The sporulation ceased abruptly with the drop in temperature.

Following the changes in temperature, various fluctuations of the relative humidity were tried but sporulation could not be induced. These results indicate that temperature is the chief influencing factor in determining the periods of sporulation, and that the drop in relative humidity which normally accompanies rises in temperature had little if any influence upon the number of spores cast.

Briefly, the results of the studies of meteorological factors affecting sporulation may be summarized as follows: temperature is a major influence in determining the periods of sporulation; sporulation occurred at all times except where the average weekly temperature was below 32° F.; heavy sporulation following cool weather, was induced by a rise in temperature above 50° F. for several hours. Fluctuations of spore cast correlated more closely with the rise and fall of temperature inside the context of the sporophore than with fluctuating temperatures outside the sporophore. The relative humidity was not a major influence on sporulation. There was no regular daily periodicity of sporulation.

CULTURE METHODS

Cultures of *Fomes pini* were obtained from spores and sporophore tissue. Difficulty was experienced at first in obtaining cultures from spores due to the methods employed in handling them. When they were collected on glass slides, the spores failed to germinate satisfactorily. Therefore, a method was devised for casting spores directly upon culture media. Sufficient malt agar was poured to barely cover the bottom of a Petri dish. A square of sterilized wire gauze was substituted for the Petri dish cover. A fresh sporophore was placed on top of this and so orientated as to bring the longitudinal axis of the tubes into a vertical position. A bell jar which had been previously sterilized by washing with alcohol, was placed over the Petri dish and sporophore. One to 2 hours were allowed for the casting of the spores after which the sporophore was removed and the regular Petri dish cover replaced. Cultures made up in this manner were remarkably free from contamination.

Spores were collected on drops of media on cover glasses which were later used for hanging-drop cultures in Van Tiegam cells. Although the spores germinated, the method did not lend itself as favorably to this study as the previously described method.

Cultures were made from the tissue of sporophores by splitting the fruiting body open and with sterile forceps and scalpel removing a small piece of the context from the freshly exposed surface. These pieces of tissue were partly embedded in agar in Petri dishes. Stock cultures were secured from these and grown on malt agar in culture tubes.

Subcultures were made by removing small pieces of mycelia near the outer edge of the mycelial mats and placing them on the fresh substrata in Petri dishes. The tool used in making transfers is described in some detail, as the author has never seen it mentioned elsewhere in the literature, though a similar instrument is used by J. L. Lowe at the University of Michigan. A six-inch No. 7 Bard-Parker handle for surgical knives was clamped solidly into one end of a piece of one-quarter inch copper tubing, 16 inches long, making a total length of 22 inches. A No. 12 Bard-Parker curved blade was then fixed into the handle. This instrument had several advantages over the ordinary needle, stab, or scalpel because it was rigid and would not bend when working with dried cultures. Furthermore the blade was sharp, which made it useful in cutting through tough mycelial mats. It was quickly usable after each sterilization if, after flaming, it was cooled by immersion in alcohol, which was then burned off. It would not break under considerable pressure. The length adapted it for use in large culture flasks and no unusual precaution is required for its care.

NUTRIENT MEDIA

Cultures were stored at room temperatures in diffuse light beneath bell-jars. All cultures forming a part of these experiments were incubated at 26° C. and in darkness except where otherwise noted.

The following is a list of the media used. No. 1-7 were prepared by the Digestive Ferments Co., Detroit, Michigan.

1. Potato Dextrose Agar (pH 5.6)
2. Prune Agar (pH 5.5)
3. Lima Bean Agar (pH 5.0)
4. Cabbage Infusion Agar (pH 7.4)
5. Bean Pod Agar (pH 5.4)
6. Corn Meal Agar (pH 6.1)
7. Malt Extract Agar (Synthetic) (pH 4.7)
8. Malt Agar (pH 5.6) (61)
9. Leonian's Medium (pH 5.5) (45)
10. Czapek's Synthetic Agar (pH 5.4) (31)
11. Czapek's Synthetic Agar (modified by Fritz) (pH 5.5) (31)
12. Maltose Agar (pH 5.7)
    10 g. maltose
    25 g. agar (shredded)
    1 l. distilled water
    The maltose and agar were dissolved by boiling. The medium was tubed, and autoclaved for 20 minutes at 15 pounds pressure.
13. Dextrose Agar (pH 5.5)
    The same formula was used as for medium No. 12 except that dextrose was substituted for maltose.
14. Lactose Agar (pH 5.6)
    The same formula was used as for medium No. 12 except that lactose was substituted for maltose.
15. Pine Wood Agar (pH 6.7)
    50 g. *Pinus strobus* L. sawdust
    25 g. agar (shredded)
    1 l. distilled water
    The sawdust was boiled for one hour with the agar and water. The medium was filtered, tubed, and autoclaved for 20 minutes at 15 pounds pressure.
16. Balsam Wood Agar (pH 5.8)
    The same formula was used as for medium No. 15 except that the sawdust from *Abies balsamea* (L.) Miller was substituted for pine sawdust.
17. Spruce Wood Agar (pH 6.1)
    The same formula was used as for medium No. 15 except that the sawdust from *Picea rubra* Link was substituted for pine sawdust.

18. Pine Wood Decoction
    The same as medium No. 15 with the omission of the agar.
19. Balsam Wood Decoction
    The same formula as medium No. 16 with the omission of the agar.
20. Spruce Wood Decoction
    The same as medium No. 17 with the omission of the agar.
21. Spruce Bark Decoction
    The same formula as medium No. 15 except that spruce bark sawdust was substituted for pine wood and the agar was omitted.
22. Malt Extract Liquid Medium
    25 g. malt extract (Difco)
    1 l. distilled water
    The malt extract was dissolved in the water, tubed and autoclaved for 20 minutes at 15 pounds pressure.

The cultures on wood blocks are described under section on culture studies on wood blocks. The pH values of the media indicated above were determined by the use of a Youden Quinhydrone apparatus. All media were used without alteration except in those experiments which were designed only to determine the effect of different pH values.

SPORE GERMINATION

The spores of *Fomes pini* were germinated by Brefeld (15) and Möller (58); each gave a brief description. Möller commented particularly on the difference in size between the early formed mycelium and the fine branching hyphae formed later, which he stated to be only 2-3 microns in diameter. He also noted the absence of clamp connections.

Description

Spores were placed on the surface of malt agar in Petri dishes for use in studying the characteristics of germination. On this medium, a high germination was obtained in 48 hours.

Upon germination, a small pore appeared at one end of the spore, and through this there emerged a germ tube, which was about one micron in width. Only one germ tube was produced, and this soon formed branches which were close to the spore and characteristically at right angles to each other (Fig. 12). The young hyphae grew very slowly at first, attaining a length of about 20 microns within 24 hours after the germ tube appeared. They acquired a total length, including the branches of the hyphae, of approximately 100 microns at the end of 48 hours. After 60 hours, they had become 200 microns in length. The hyphae are

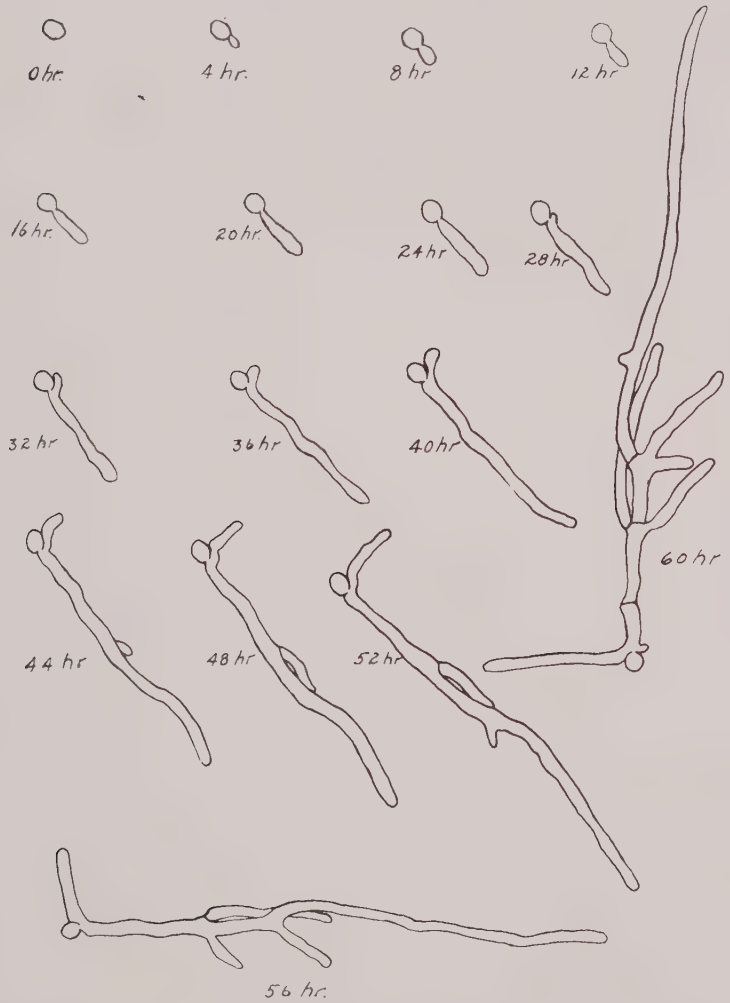

Fig. 12. Germination of a basidiospore of *Fomes pini* showing development at four-hour intervals. x 650. Camera lucida.

about 3 microns in diameter when first formed but increase in size for approximately 2 days until they reach a diameter of 5 microns. At this time, they begin to branch quite profusely. The hyphae swell before they branch and these swellings give the older parts an irregular contour. In branching, the hyphae are constricted at the base and those of the young mycelium do not anastomose freely although this seems to be a common occurrence when they become older. Clamp connections were never observed on the hyphae of *Fomes pini* in either monosporous, heterosporous or tissue cultures, irrespective of their age. This agrees with statements by Möller (58) and Fritz (31). Clamp connections have been seen on hyphae in pocket-rotted wood such as were sketched by Hubert (43). However, these may have been a part of the mycelium of a secondary fungus and hence should not be ascribed to *Fomes pini.*

Germination on Various Substrata

Various substrata were used in this study with the idea of determining the effect of different foods on the amount and speed of germination. The spores were cast directly from the fruiting bodies upon 30 different substrata in the manner previously described. These included the media described in the section on nutrient media and in addition, plain agar (15 g. agar and 1 liter distilled water), rain water, and distilled water with traces of hydrochloric and lactic acids. Spores were also cast upon thin cross sections of the heartwood and sapwood of *Pinus strobus* L. and *Picea rubra* Link which had been placed upon slides in Petri dishes. These substrata are listed in table 5 together with data concerning germination. The germination data were based upon a count of 200 spores in each of 2 Petri dishes, a total of 60 dishes. An analysis reveals that wherever the higher germination percentages prevailed, a large amount of sugar was present. Moreover, certain sugars seemed more favorable than others. On two substrata, malt extract and Leonian's medium, both of which contain a large amount of maltose, germination amounted to more than 21 per cent within the first 24 hours and 91 per cent within 3 days. Potato dextrose agar did not encourage early germination but the rate increased rapidly. At the end of 3 days it equalled that of maltose (1 per cent). This suggests enzymatic action on the starch as the germination on dextrose, when used alone, was comparatively low. Lactose (1 per cent) was also relatively unfavorable compared with maltose-containing media.

Although germinated spores were found on the liquid media, the curving surface in the hanging drop cultures and the moving surface in the Petri dish cultures impaired the accuracy of the count. The averages were not recorded. The substrata in which

traces of acids were introduced supported no germination. Although spore germination was observed upon the wood sections, the visability was so poor, due to the opaque substratum, that no count was made.

The results of this study indicate that those media which contain readily available sugars, especially maltose, favor an early as well as high percentage of germination.

TABLE 5. *Spore germination of Fomes pini on various substrata*

Substrata	pH	Per Cent Germination by Days			
		1	2	3	4
Potato dextrose agar	5.6	2.3	82.9	91.0	.....*a*
Prune agar	5.5	0.5	30.3	57.2	59.0
Lima bean agar	5.0	2.5	54.5	57.9	58.0
Cabbage agar	7.4	0	0	0	0
Malt extract agar (syn.)	4.7	1.0	2.4	8.7	10.6
Malt extract agar (reg.)	5.6	21.1	88.8	93.2	.....*a*
Bean pod agar	5.4	3.2	67.8	71.8	75.7
Corn meal agar	6.1	0.2	2.9	6.5	17.5
Leonian's agar	5.5	27.9	80.7	91.7	.....*a*
Czapek's agar (reg.)	5.4	1.4	16.8	31.9	39.2
Czapek's agar (mod.)	5.5	0.5	34.7	62.3	79.9
Maltose agar (1%)	5.7	.....	.....	86.5	.....*a*
Dextrose agar (1%)	5.5	.....	.....	16.3	21.6
Lactose agar (1%)	5.6	.....	.....	23.8	45.7
Pine agar	6.7	.....	.....	1.0	1.5
Balsam agar	5.8	.....	.....	68.4	77.7
Spruce agar	6.1	.....	.....	13.0	12.7
Plain agar	7.0	.....	.....	.....	0
Pine decoction	.....	.....	.....	.....	Germ.*b*
Spruce decoction	.....	.....	.....	.....	Germ.*b*
Balsam decoction	.....	.....	.....	.....	Germ.*b*
Spruce bark decoction	.....	.....	.....	.....	Germ.*b*
Lactic acid (trace)	.....	.....	.....	.....	0
Acetic acid (trace)	.....	.....	.....	.....	0
Hydrochloric acid (trace)	.....	.....	.....	.....	0
Rain water	.....	.....	.....	.....	Germ.*b*
Pine heartwood sections	.....	.....	.....	.....	Germ.*c*
Pine sapwood sections	.....	.....	.....	.....	Germ.*c*
Spruce heartwood sections	.....	.....	.....	.....	Germ.*c*
Spruce sapwood sections	.....	.....	.....	.....	Germ.*c*

a Hyphal growth had become great enough to obscure ungerminated spores.

b Spores had germinated but the counts were inaccurate due to liquid substrata.

c A few spores had germinated but no records were made owing to the difficulty of securing accurate counts on an opaque substratum.

Acidity

The study of spore germination on various substrata, primarily undertaken for the purpose of determining the influence of different foods upon germination, also indicated the direct influence which the acidity of the substratum exerts. It may be noticed in table 5 that those substrata, the pH of which was below 5.0 or above 6.0, failed in any case, to support a germination higher than 17.5 per cent. The results on the substrata whose pH values were between 5.0 and 6.0, though not uniform, averaged 81.0 per cent germination. Inasmuch as the various foods contained in the media also affected germination, another study was made with the acidity of the medium as the only variable. Plain agar was used which was adjusted by adding lactic acid or potassium hydroxide.

The plain agar was first autoclaved in small Erlenmeyer flasks. To these flasks, sufficient amounts of concentrated lactic acid or potassium hydroxide were added to produce a wide range of acidities, which are listed in table 6. Two Petri dishes of agar of each acidity were poured and spores were cast directly upon the medium. They were incubated at 26° C. and observations of 200 spores on each medium were made daily over a period of 1 week.

In this study food was not included in the substrata. No germination was obtained above a pH value of 6.0 and germination decreased sharply below 5.0 pH.

TABLE 6. *Spore germination of Fomes pini on plain agar at various acidities*

pH of substrata	Percentage germination
4.0	22
5.0	71
5.5	86
6.1	0
6.5	0
7.0	0
7.6	0
8.0	0

It seems safe to conclude that the acidity of the substrata has an important influence upon the spore germination of *Fomes pini* and further that the most favorable acidity lies between 5.0 and 6.0 pH.

CULTURE STUDIES ON VARIOUS MEDIA

Cultures of *Fomes pini* were derived from several sources as listed in table 7. Each of these was grown on malt agar in Petri dishes and later compared with each other for culture characteristics. The cultures were numbered and will be referred to by their respective numbers throughout the remainder of this paper.

In growth characteristics the various cultures were quite similar. All produced fluffy, tufted surfaces with colors which varied from Pinard Yellow[9] in the younger portions through Buff Yellow and Yellow Ochre to Antique Brown on the oldest parts of the cultures near the inoculum. The cultural characteristics of *Fomes pini* have been so well reported and portrayed by Fritz (31) that a repetition of the description is unnecessary. The "expansions" in the hyphae which Fritz (31) describes as mere enlargements were common. In addition to these, cells which resembled typical chlamydospores were found. These cells were distinguished by a thick wall and dense protoplasmic contents which definitely differentiated them from the normal vegetative cells (Fig. 13). They have been found both as terminal and intercalary cells on the hyphae of all the cultures whether of monosporous or heterosporous origin. The number of chlamydospores in the cultures varied greatly without any apparent differences in cultural conditions.

Clamp connections were never found in culture. No distinctive differences were noticed between different cultures whether they originated from monosporous or heterosporous mycelia or from sporophore tissue.

No fertile fruiting bodies were obtained in culture.

Various Substrata

The substrata used in this study include those listed in table 8. Three Petri dishes containing 25 cc. of each medium were inoculated with tissue from culture 304.

A thick, dense, rapid-growing mycelium was developed on a few media which included potato dextrose agar, malt extract (solid and liquid), Leonian's medium and Czapek's synthetic agar (modified). All of these media contained a high percentage of sugar and had a pH value of either 5.5 or 5.6. Media of this class were also found to be favorable for the germination of spores (Table 5). A thin, rapid-growing mycelium was supported by several media irrespective of the kind of food and the acidity. The depth of color of the mycelium seemed independent of the rate or density of the hyphal growth.

[9] All names of colors are taken from Color Standards and Color Nomenclature by R. Ridgway, 1912.

TABLE 7. *Sources of cultures*

Culture Number	Original inoculum	Source	Locality
101–107	Single spore	Annual sporophore on log of *Picea rubra*	Old Forge, New York.
108–109	Single spore	Annual sporophore on log of *Picea rubra*	Clearwater, New York.
110–121	Single spore	Perennial sporophore on log of *Picea rubra*	Old Forge, New York.
201–204	Single spore	Annual sporophore on log of *Picea glauca*	Warrensburg, New York.
301–304	Tissue	Perennial sporophore on log of *Pinus monticola*	Tatah County, Idaho.
401	Tissue	*Picea canadensis*	Timagami Forest Reserve, Ontario.
601	Tissue	Perennial sporophore on *Pseudotsuga taxifolia*	Spirit Lake, Washington.
610	Tissue	*Pinus contorta*	Wyoming.
701	Tissue	Host unknown	Holland.
702	Tissue	*Pinus Maritima*	Bordeaux, France.
955	Tissue	*Picea rubra*	Lac Claude, Gaspé, Quebec.
975	Tissue	Picea species (root)	Gaspé, Quebec.
1101, 1103	Tissue	*Picea rubra*	Cranberry Lake, New York.
1105	Tissue	*Pinus strobus*	Source unknown.
1251	Tissue	Coniferous log (sapwood)	Cameron Lake, V. I., B. C.
1253	Tissue	Pseudotsuga log	Parksville, V. I., B. C.
2554	Tissue	*Psuga heterophylla*	Coolin, Priest Lake, Idaho.

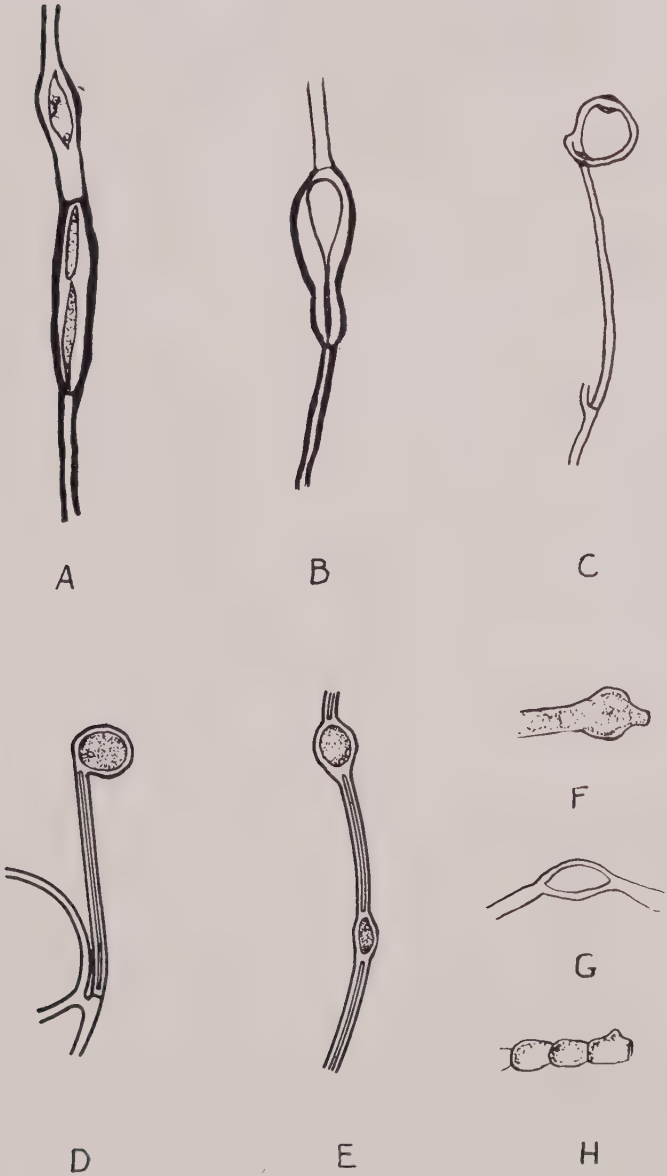

Fig. 13. Characteristic mycelial structures of *Fomes pini.* (a-b) Expansions in hyphae; (c) helicoid hyphae; (d) terminal chlamydospore; (e) intercalary chlamydospores; (f-g) expansions in hyphae; (h) rounded cells. x 650. Camera lucida.

TABLE 8. *Mycelial growth of Fomes pini on various substrata. Measurements of average radial growth*

Substrata	pH	Growth in Millimeters at 3 Day Intervals							Appearance	
		3	6	9	12	15	18	21	Density	Color
Potato dextrose agar	5.6	2	4	10	16	22	29	35	Heavy	Brown
Prune agar	5.5	3	6	12	19	24	31	38	Medium	Brown
Lima bean agar	5.0	3	5	8	10	13	16	19	Medium	Ochre
Cabbage agar	7.4	1	2	4	6	8	10	12	Medium	Lt.yellow
Malt extract (syn.) agar	4.7	1	3	7	11	15	19	23	Light	Brown
Malt extract (reg.) agar	5.6	3	5	11	15	20	25	30	Heavy	Ochre
Bean pod agar	5.4	1	2	5	8	11	14	17	Heavy	Brown
Corn meal agar	6.1	1	4	8	15	20	26	32	Light	Lt.yellow
Leonian's agar	5.5	2	4	10	16	21	27	32	Heavy	Brown
Czapek's (reg.) agar	5.4	1	4	10	17	22	29	33	Light	Yellow
Czapek's (mod.) agar	5.5	1	4	12	19	26	33	40	Heavy	Ochre
Maltose (1%) agar	5.7	2	6	13	18	25	32	37	Medium	Ochre
Dextrose (1%) agar	5.5	3	8	16	21	27	33	39	Light	Yellow
Lactose (1%) agar	5.6	1	6	13	19	25	32	38	Light	Yellow
Pine agar	6.7	1	1	3	8	11	14	18	Light	White
Balsam agar	5.8	2	6	12	17	22	28	33	Light	Yellow
Spruce agar	6.1	1	1	3	5	6	8	10	Light	White
Malt extract liquid	...	5	11	15	19	24	29	34	Thick	Brown
Pine decoction	....	3	7	9	11	14	15	15	Light	White
Balsam decoction	....	3	7	11	14	18	21	22	Light	Buff
Spruce decoction	....	1	2	4	6	8	10	11	Light	White
Spruce bark decoction	....	2	5	8	11	15	18	20	Light	Buff
Na Cl (.4%) liquid	....	0	0	1–	1–	1–	1–	1–	.....	.....
KH_2PO_4 (.4%) liquid	....	0	0	1–	1–	1–	1–	1–	.....	.....
K_2HPO_4 (.4%) liquid	....	0	0	0	0	0	0	0	.....	.....
$Cu\ SO_4$ (.4%) liquid	....	0	0	0	0	0	0	0	.....	.....
$Na_2\ CO_3$ (.4%) liquid	....	0	0	0	0	0	0	0	.....	.....
$Hg\ Cl_2$ (.4%) liquid	....	0	0	0	0	0	0	0	.....	.....
H Cl (.4%) liquid	....	0	0	0	0	0	0	0	.....	.....
C_2H_5OH (.4%) liquid	....	0	0	0	0	0	0	0	.....	.....
Distilled water	....	0	0	0	0	0	0	0	.....	.....

Acidity

The effective acidity of malt agar was adjusted by the addition of small amounts of concentrated lactic acid or potassium hydroxide. A series of cultures was made ranging from 2.95 pH to 7.90 pH with intervals of approximately 0.5 pH. Three cultures were made at each acidity with hyphae from culture 304 used as the inoculum. The extent of the mycelial development was determined by measuring the average radial growth. The measurements of the mycelia at each acidity were averaged and the results recorded in table 9.

The mycelial growth of *Fomes pini* is not greatly affected by changes in the acidity of the substratum within wide limits. There is a difference of but 13.9 per cent in growth between the pH values of 3.85 and 7.90. *Fomes pini* mycelium in culture is evidently not specific in its requirements in regard to the acidity of the substrata.

TABLE 9. *Mycelial growth of Fomes pini culture 304 on malt agar of different hydrogen ion concentrations as measured by average radial growth*

pH	Growth in Millimeters at 3 Day Intervals						
	3	6	9	12	15	18	21
2.95	1	4	7	10	14	17	19
3.35	3	7	11	15	19	23	27
3.85	5	9	14	19	23	28	31
4.30	5	11	16	21	25	30	33
4.85	5	10	15	20	24	29	33
5.25	5	11	15	20	24	29	33
5.55	6	11	16	21	25	30	34
6.10	6	12	17	23	28	33	36
6.60	6	12	17	23	28	33	36
7.15	6	12	18	24	28	33	36
7.90	3	9	16	23	28	33	36

Temperature

Twenty-five cubic centimeters of malt agar were poured into each of 27 Petri dishes and inoculated with tissue from culture 304. The subcultures were divided into 9 groups of 3 cultures each, to be incubated at various temperatures. In order to prevent uneven dessication at the different temperatures, each group of 3 subcultures, together with an open dish of water, was placed in tightly covered tin cans, 15 cm. long by 11 cm. in diameter.

The cultures were incubated in darkness at the various temperatures recorded in table 10. Measurements of the resulting mycelial growth were made.

The optimum temperature in this experiment proved to be 25° C. From this optimum, the extent of growth tapered off gradually in those cultures incubated at lower temperatures, but for higher temperatures than 25° C. the mycelial growth decreased very sharply. The minimum temperature for growth lies between 1° and 6° C. The maximum temperature lies between 30° and 35° C.

Light

Fomes pini (Culture 304) was grown upon the 17 solid media described in the section on nutrient media. Four Petri dish cultures were made of each medium. Half of the cultures (2 of

TABLE 10. *Mycelial growth of Fomes pini on malt agar at various temperatures. Measurements were made of average radial growth*

Degrees Centigrade	Growth in Millimeters at 3 Day Intervals							
	3	6	9	12	15	18	21	24
1	0	0	0	0	0	0	0	0
6	0	0	1–	1–	1	1	1	2
10	0	1–	1–	1	2	5	8	10
15	0	1	3	6	10	13	18	22
21	1–	6	11	17	24	30	35	39
25	3	9	16	21	27	33	39	44
30	0	1–	1–	1	2	3	5	6
35	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0

each medium) were incubated in light and the other half in darkness. At the end of 2 weeks, the cultures which grew under the influence of light were slightly darker in color and the aerial hyphae were somewhat more compact than those which grew in darkness.

A further study was made to determine the effect of sunlight upon mycelial growth. Malt extract agar was poured into 3 stender dishes, 2.5 cm. high and 5 cm. in diameter and inoculated with tissue from *Fomes pini* (Culture 304). These were incubated until they had produced a mycelial mat 4 cm. in diameter. One of the stender dishes was covered with a piece of fused quartz glass, a second with ordinary window glass, and a third was placed in a tight tin box to prevent the entrance of light. These 3 were placed on an outside window ledge. The cultures which were covered by quartz glass and window glass received sunlight only through these substances. After an exposure to sunlight for 5 hours the cultures were returned to the incubator for 3 days and then exposed for another 5 hours to the sunlight and again returned to the incubator.

At the end of this treatment, the culture which had been kept in darkness had the characteristic fluffy, tufted surface and an ochre color. The culture which was exposed to sunlight through window glass was only slightly deeper in color than that kept in darkness. The culture which had been covered with quartz glass differed in several ways from the others. The color had become a dark shade of brown; there was but little aerial hyphae; no

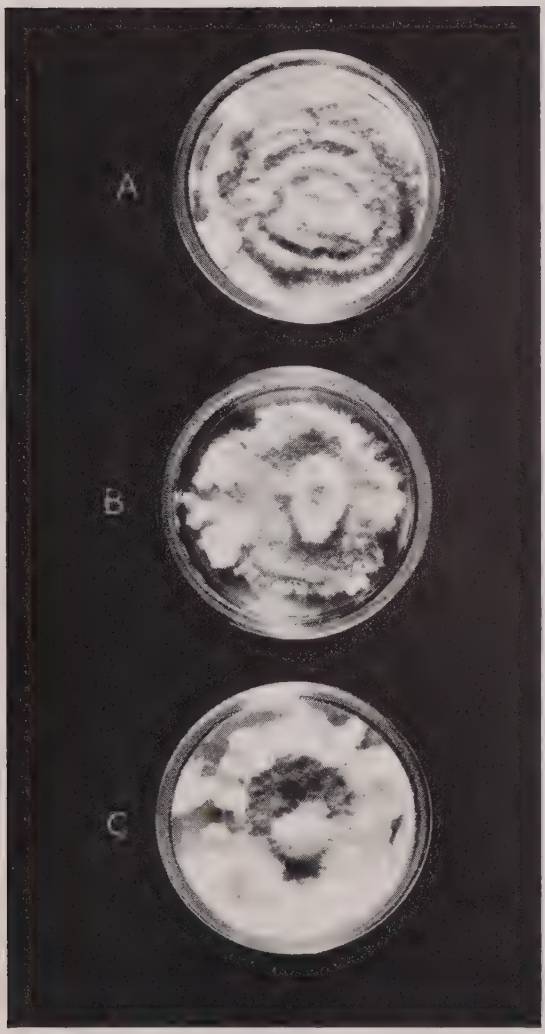

Fig. 14. Cultures of *Fomes pini* upon malt agar incubated under similar conditions except as follows: (a) Exposed to sunlight as transmitted through quartz glass for 2 five-hour periods; (b) exposed to sunlight as transmitted through window glass for 2 five-hour periods; (c) kept in darkness.

tufted cottony mycelium was apparent; the surface of the mycelium was zonate. There were 2 zones of hyphae closely appressed to the surface of the substratum, with low intervening ridges of sparse aerial mycelium. The closely appressed zones corresponded exactly with the margin of growth at the time that the culture was exposed to the sunlight. These features are shown in figure 14.

According to Coblentz (18), fused quartz glass transmits 92 per cent of the light rays from 360 millimicrons to 260 millimicrons in length, whereas window glass transmits none of the shorter wave lengths. The results indicate, that ultra violet light suppresses and darkens the aerial mycelium to a greater extent than the rays of the visible spectrum.

CULTURE STUDIES ON WOOD BLOCKS

One Species of Wood Inoculated with *Fomes pini* Secured from Various Hosts

Fomes pini cultures obtained from different sources and associated with different types of decay were employed to inoculate blocks of red spruce for the purpose of comparing the resultant decays. No attempt was made to secure maximum decay. All cultures were grown under similar conditions.

A sound red spruce was felled and a ten-foot length cut from the trunk. A clear section of the heartwood was sawed into 210 one-inch cubes. These blocks were divided into 21 groups and the blocks in each group were numbered from 1 to 10, with an ordinary lead pencil. They were weighed to the nearest thousandth of a gram and the volumes secured by measurements taken with a micrometer. From these weights and volumes, specific gravities were computed. The cubes were boiled in water until they sank and then placed in 21 lipless beakers, 10 cubes in each beaker (Fig. 15).

Three pieces of glass tubing, 2 cm. in diameter, were placed on the bottom of each beaker. These were covered with a thin layer of absorbent cotton which hung down around the glass tubing to serve as a wick. The bottom of the beaker was then covered with water to a depth of about one centimeter. On top of the glass tubing and absorbent cotton, the 10 cubes of red spruce were arranged in 3 layers. The lowest layer was comprised of 4 cubes placed tightly together; the middle and top layers were each made up of 3 blocks with a wide triangular space between the blocks in each layer. Each beaker was covered with a layer of absorbent cotton and a Petri dish cover, after which it was autoclaved for 30 minutes at 15 pounds pressure. The cubes were inoculated

Fig. 15. Culture of *Fomes pini* upon one-inch cubes of *Picea rubra* Link. x 1.

with *Fomes pini* by placing the inoculum at the center on the upper surface of the lowest layer of cubes. In this way, the inoculum was not more than one inch from the farthest cube.

These inoculations were made with 6 different cultures of *Fomes pini*. Three beakers, each containing 10 uninoculated blocks, were used as a control. Eighteen beakers, containing 10 blocks each, were grouped into 6 series of 3. Each series was inoculated with one of the following cultures: Culture 955 from *Picea rubra* Link from Quebec, 1101 and 1103 from *P. rubra* Link from New York, 1105 from *Pinus strobus* L., locality unknown, 303 and 304 from *P. monticola* D. Don from Idaho. The cultures were incubated at 26° C. Within 3 weeks after inoculation, a web of hyphae had covered all of the blocks in the successful cultures. The hyphae developed into a thin, tufted, brown mycelium. Later the surfaces of the blocks became pitted similar to typical pocket-rotted wood. The rot did not extend into the wood to any great depth however. After 9 months incubation, the decay had penetrated longitudinally about 3 mm. while the radial and tangential penetration was usually less than 1 mm. All decay was of the pocket-rot type.

For the purpose of determining the extent of decay quantitatively, one culture from each series of 3 and one control culture, as described above, were removed from the incubator at the end of 3 months. The remaining cultures were left for further development. Of the cultures removed, 1101, 1103, and 303 had failed to develop. The extent of decay was measured in 2 ways, i. e., loss in specific gravity and decrease in absolute crushing strength. The change in specific gravity was determined by weighing each block to the nearest thousandth of a gram at oven-dry weight before and after the incubation period. Both weights were based upon the original oven-dry volume for the purpose of computing the change in specific gravity. The absolute crushing strength of the oven-dry blocks was then obtained by means of a Riehle Testing Machine (maximum load 50,000 pounds, calibrated to 10 pounds).

At the end of 6 months another culture from each of the original series of 3 was removed from incubation. All of these including numbers 1101, 1103, and 303 had grown and produced decay. The specific gravities and the crushing strengths of these cubes were secured in a manner similar to that just described.

At the end of 9 months, the remaining cultures were examined and decay was found to have developed in all the cultures. The amount of decay was measured as before by changes in specific gravities and crushing strengths. The results of these quantitative measurements are summarized in table 11.

TABLE 11. *Changes in specific gravity and crushing strength of wood of Picea rubra Link during incubation for various periods with Fomes pini secured from different hosts. Each figure is based on an average of ten blocks*

Culture	Original host	Average Per Cent Decrease in Specific Gravity			Average Per Cent Loss or Gain in Crushing Strength Compared with Control in Pounds Per Square inch In Transverse Section			
		3 mo.	6 mo.	9 mo.	3 mo.		6 mo.	9 mo.
					Gain	*Loss*	*Loss*	*Loss*
Control	.....	.98	2.62	2.87	....	....	....	.....
955...	*Picea rubra* Link.....	3.27	6.58	10.27	0.9	....	14.0	40.9
1101...	*Picea rubra* Link.....	....	6.20	10.28	....	....	2.0	33.7
1103...	*Picea rubra* Link.....	....	3.61	4.95	....	....	3.1	9.3
1105...	*Pinus strobus* L.....	3.70	5.29	7.71	1.0	....	10.7	40.1
303...	*Pinus monticola* D. Don.	....	4.16	6.52	....	....	8.4	20.8
304...	*Pinus monticola* D. Don.	2.14	3.89	7.83	....	0.3	1.6	29.4

The losses in specific gravity increased with the period of time during which the cultures were incubated. Further, the loss increased rather evenly within each series of blocks. Between series inoculated with different cultures, however, there was a wide difference in losses in specific gravity, which ranged from 4.95 per cent to 10.28 per cent at the end of 9 months. The greatest variation occurred between series which were inoculated with cultures from the same species of host, i. e., *Picea rubra*. The losses in the series inoculated with cultures secured from *Pinus strobus* and *P. monticola* were intermediate.

The crushing strengths of the blocks, regardless of the origin of the inoculum, remained approximately the same at the end of 3 months. This agrees with Colley's (19) results in which he found that sticks infected with the incipient stage of *Fomes pini* were as strong or stronger than the sound wood. Liese (46) also found that *Fomes pini* caused only very slight damage to pine blocks upon which the fungus had been incubated 4 months. At the end of 9 months, however, there were large losses in the crushing strengths which compared favorably with the relative losses in the specific gravities. In comparing the losses in crushing strength, it is again apparent that there is a greater difference between the strengths of blocks inoculated with *Fomes pini* from the same species of host than between blocks which were inoculated with material from different host species.

Various Species of Woods Inoculated with *Fomes pini* Secured from One Host

A further investigation into the decay of wood by *Fomes pini* was carried out with the idea of determining whether a culture taken from a single host would produce different types of decay when cultured on different woods.

Wood blocks, 8 x 2 x 2 cm. were cut from 6 different woods, as follows: *Pinus strobus* L., *Picea rubra* Link, *Abies balsamea* (L.) Mill., *Larix laricina* (DuRoi) Koch, *Thuja occidentalis* L., *Tilia glabra* Ventenat. Four blocks were cut from both heartwood and sapwood of each of the first 5 woods named above, whereas only the sapwood was utilized in *Tilia glabra* Ventenat.

The blocks were placed in distilled water in separate Erlenmeyer flasks, and an aspirator attached for 2 hours in order to partly exhaust the air after which each group of 4 blocks was autoclaved in separate containers. The blocks were inoculated by placing them on a well developed mycelial mat which had been produced in the following way. Sections of 2 cm. glass tubing were placed on the bottom of one-liter, wide-mouth culture flasks and 125 cc. of malt agar poured over them. The flasks and agar were then autoclaved for 20 minutes at 15 pounds pressure. As they were cooling, the flasks were shaken sufficiently to dash the half-cooled agar against the sides of the glass tubing thus depositing a thin coating of solidified agar. This surface coating of malt agar was inoculated with *Fomes pini* (Culture 304). Cultures were incubated at 26° C. for a month until the agar surface was completely covered by a thick mycelial mat.

The blocks of wood were transferred directly from the containers in which they had been sterilized to the month-old cultures in the flasks. They were arranged on the mat of *Fomes pini* mycelium which in turn was supported by the glass tubing. The cultures were allowed to incubate for 7 months at 26° C. Figures 16, 17, and 18 illustrate these cultures at the end of the period of incubation.

During the first 2 weeks after inoculation, a growth of mycelium completely covered all the blocks with the exception of cedar heartwood. After the incubation period, a microscopic examination was made of the different woods which had been in culture. Hyphae were found in all of the blocks except the heartwood of *Thuja occidentalis*. In all cases, the hyphae were characterized by expansions similar to those found in culture on synthetic media and illustrated in figure 13. The characteristics of the aerial mycelium and the wood decay which developed are summarized in table 12.

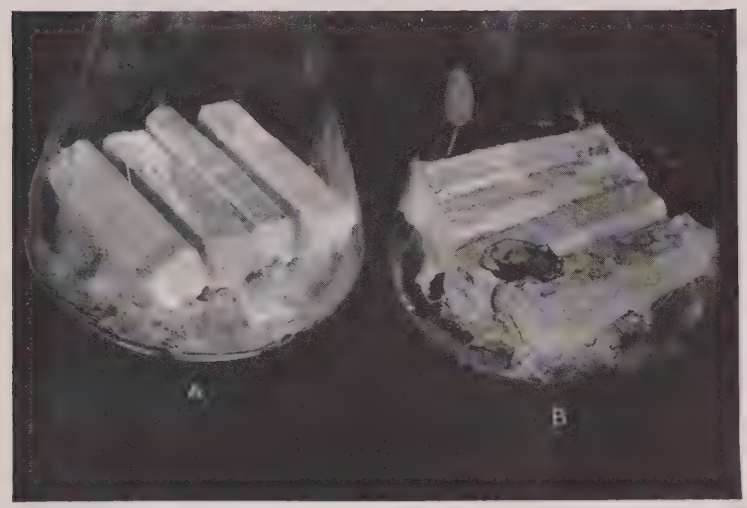

Fig. 16. *Fomes pini* on blocks of *Picea rubra* Link in culture. x ⅓. (a) Sapwood of *Picea rubra* Link; (b) heartwood of *Picea rubra* Link, showing a rudimentary sporophore.

Fig. 17. *Fomes pini* on blocks of *Pinus strobus* L. and *Thuja occidentalis* L. x ⅓. (a) Heartwood of *Pinus strobus* L.; (b) sapwood of *Thuja occidentalis* L. showing wide brownish-red lines on sides of blocks.

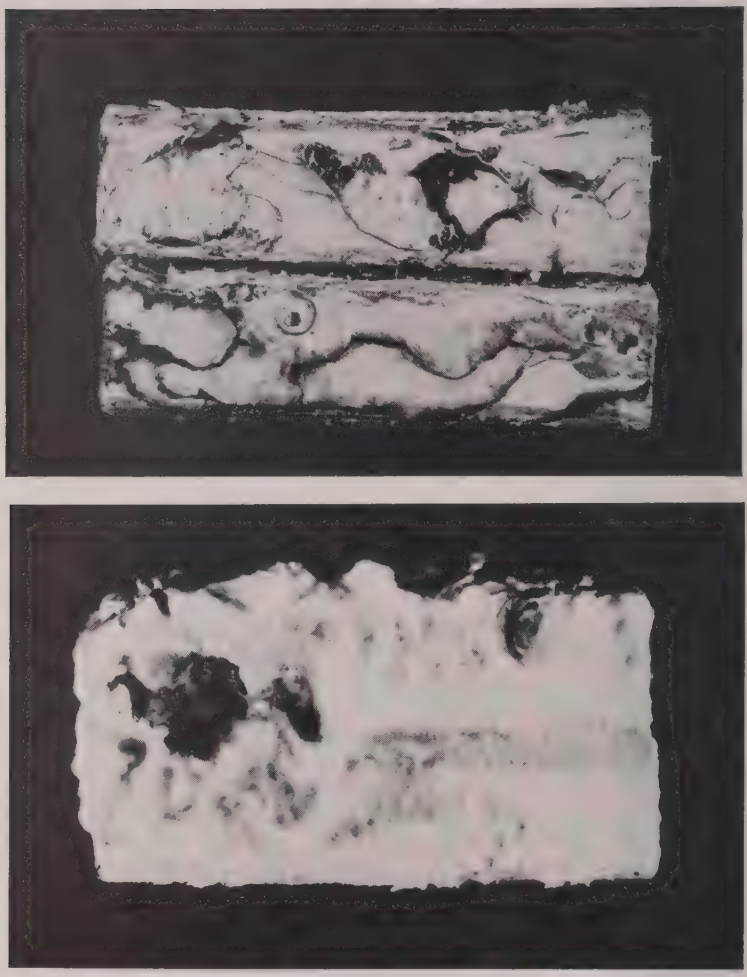

Fig. 18. Mycelial growth of *Fomes pini* on wood blocks. x 1. (Above) Sapwood of *Abies balsamea* (L.) Miller. Numerous brownish-red lines occur over surface. (Below) Heartwood of *Larix laricina* (DuRoi) Koch. A rudimentary sporophore appears on top of blocks.

TABLE 12. *Decay of different woods produced by Fomes pini originating at one source*

Wood		Mycelium	
Species	Condition	Density	Surface characters
Pinus strobus.... heartwood.	Red with a few white pockets.	Thin.....	No brown coloration (Fig. 17a).
Pinus strobus.... sapwood.	Not discolored and apparently sound.	Thin.....	Small brown mycelial mats.
Picea rubra..... heartwood.	White pockets throughout blocks.	Thick....	Scattered brown mycelial mats. Rudimentary sporophore* (Fig. 16b).
Picea rubra..... sapwood.	White pockets throughout blocks.	Thin.....	No brown coloration (Fig. 16a).
Abies balsamea... heartwood.	Spring wood completely decayed; ring scale.	Thick....	Several brown mats. Rudimentary sporophores.
Abies balsamea... sapwood.	Ring shake pronounced.	Medium..	Many brown mats. Wide brownish-red lines (Fig. 18).
Larix laricina.... heartwood.	Many white pockets in spring wood.	Thick....	Rudimentary sporophores present (Fig. 18).
Larix laricina.... sapwood.	Coalesced white pockets forming ring scale.	Thin.....	Brownish-red lines.
Thuja occidentalis heartwood.	Wood sound. No hyphae present in wood.	None....	None.
Thuja occidentalis sapwood	Whitened by decay to depth of 2 mm.	Medium..	Brownish-red lines 1–10 mm. wide (Fig. 17b).
Tilia glabra..... sapwood.	Wood apparently sound.	Medium..	Brownish-red lines 1–4 mm. wide.

* Based on the woody texture of the mycelial outgrowths.

In the section on the description of the sporophore, various types of decay were described under the names red rot, pocket rot, and ring scale. These characteristic types of decay were produced by subcultures from the one individual mycelium of *Fomes pini*, growing upon the several species of wood used. The reddening of the wood and a few white pockets, which developed in white pine heartwood, is typical of red rot (Fig. 19). The slight discoloration and numerous white pockets formed in the red spruce heartwood are similar to those commonly found in that wood in nature and called pocket rot (Fig. 20). The ring scale associated with *Fomes pini*, especially in the western woods, developed in balsam heartwood (Fig. 21).

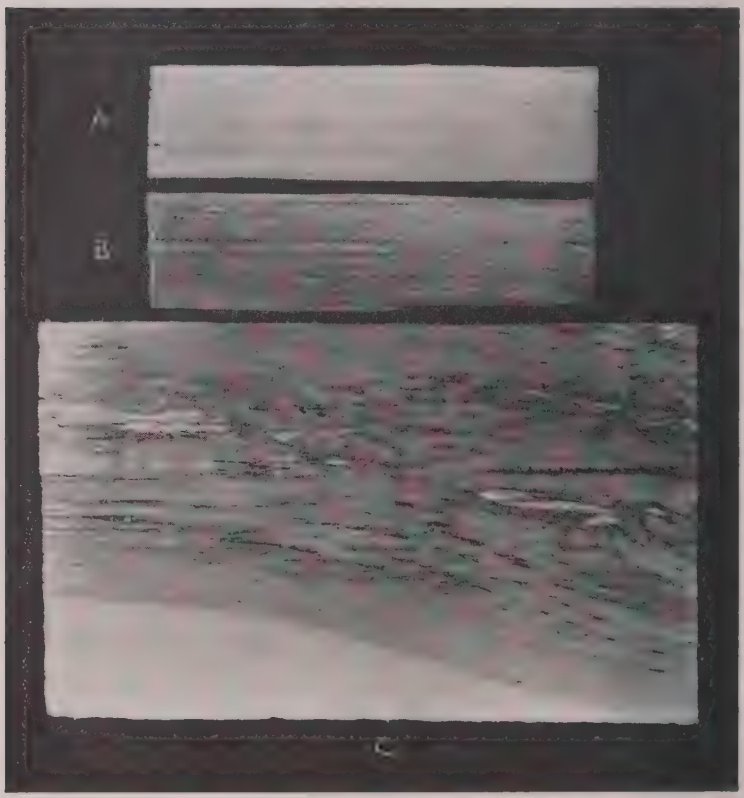

Fig. 19. Heartwood of *Pinus strobus* L., longitudinal section. x 1. (a) Sound wood; (b) wood block showing red rot produced in culture by *Fomes pini*; (c) sections of a board containing red rot produced naturally.

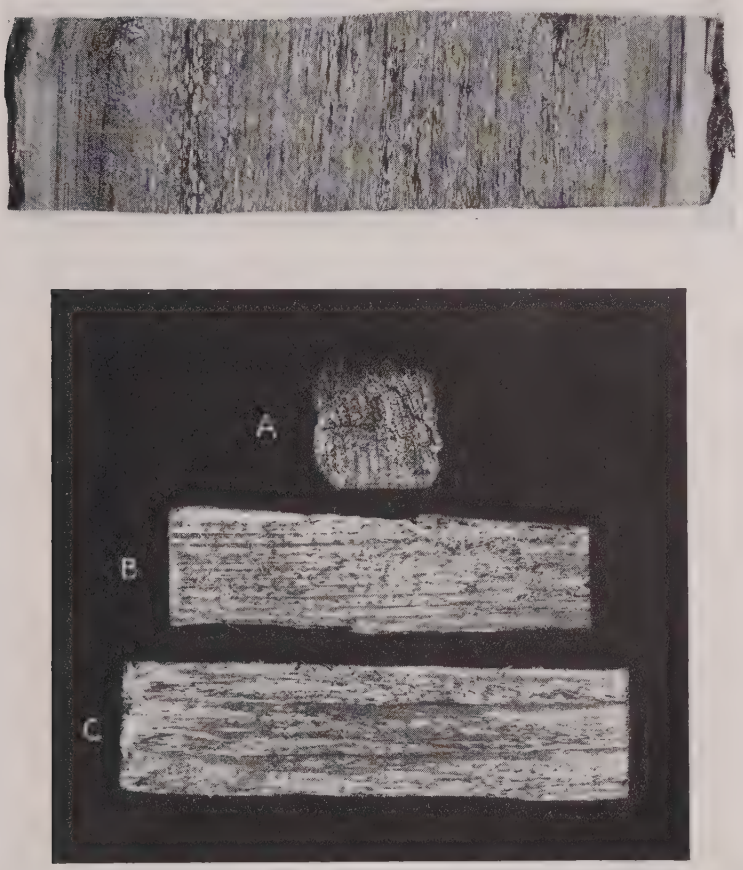

Fig. 20. (Above) Longitudinal section of *Picea rubra* Link with pocket-rot found under natural conditions. x 2/5. (Below) Wood blocks showing pocket-rot produced in culture at 26° C. by *Fomes pini*, x 1. (a) Transverse section of heartwood of *Picea rubra*; (b) longitudinal section of heartwood; (c) longitudinal section of heartwood of *Larix laricina* (DuRoi) Koch.

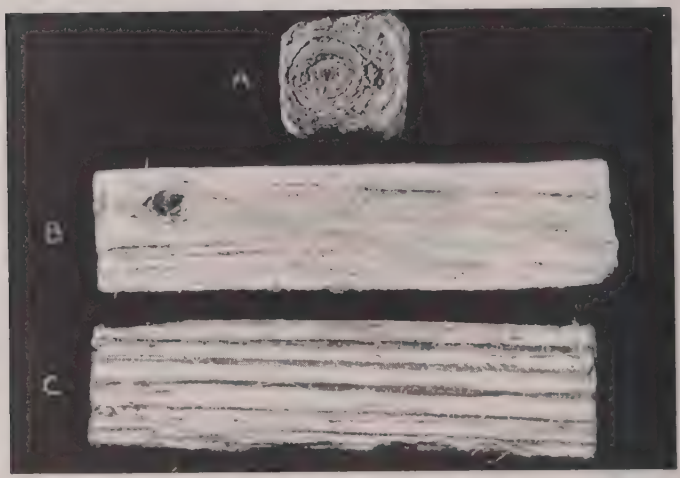

Fig. 21. (Above) Transverse section of *Pinus ponderosa* Lawson with ring scale condition. Photo by Boyce. (Below) Wood blocks showing ring scale produced in culture by *Fomes pini*. x 1. (a) Transverse section of heartwood of *Abies balsamea* (L.) Miller; (b) longitudinal section of heartwood of *A. balsamea* (L.) Miller; (c) longitudinal section of sapwood of *Larix laricina* (DuRoi) Koch.

Together with the typical wood decays associated with the names, red rot, pocket rot, and ring scale, there occurred many intergradations. For instance a few white pockets formed in the white pine somewhat similar to those in red spruce. Furthermore, a pocket rot, which appeared in larch heartwood (Fig. 20), tended to follow the spring wood of the annual rings similar to a ring shake. In the sap wood of this species (Fig. 21), the pockets in the spring wood coalesced and gave the typical ring shake appearance.

The ability of subcultures from a single mycelium of *Fomes pini* to produce, under controlled conditions, the different types of decay associated with the fungus in different hosts in nature, cannot be questioned. Hence it seems logical to assume that the one organism may cause these different types of decay under natural conditions and that these different types of decay are not characteristic of different strains of the same fungus.

DISCUSSION

Faull (28) has recently emphasized the fact that the number of hosts of a disease-causing organism is significant of its importance. He points out that the reason for the great importance of *Fomes pini* from the foresters' viewpoint, is the destruction which it causes to such a wide variety of hosts (Table 1). The hosts are so numerous that in many instances even in mixed stands, the majority of the component species are affected. The occurrence of *Fomes pini* only in the heartwood of living trees, as indicated in this paper, has a practical significance. Wounds in the tree which do not expose heartwood may be highly resistant to attack. Further, the smaller the amount of heartwood in the stubs resulting from pruning, the less would be the danger of infection.

The presence of many sporophores implies the production of an abundance of spores. It is by this means, namely, wind-disseminated spores, that the majority of forest fungi are spread.

It seems logical to expect that periods of high sporulation will also prove to be periods of greatest danger from infection. Boyce (9) and Hole (42) have indicated that infection usually occurs through broken branch stubs and numerous observations on this point have been recorded. The author has frequently observed conditions which would indicate this type of infection. During the periods of high sporulation, the avoidance of fresh wounds such as those made by pruning would, therefore, seem advisable. These heavy sporulation periods occur in early spring and late fall in central New York. The formulation of a definite policy for management requires further data regarding the longevity of the spores and the exact type of branch stubs which are susceptible to infection.

The results of culture studies on various kinds of wood showed that subcultures of the same mycelium of *Fomes pini* may cause the characteristic type of decay commonly associated with that wood under normal conditions. Since *Fomes pini* can be transferred from one wood to another in culture and produce different types of decay depending on the kind of wood, it has seemed logical to conclude that it also passes from one kind of host tree to another in the forest. This might be of considerable importance in the control of red rot in pine stands located in close proximity to spruce. Sporophores are produced in greater abundance upon spruce than on pine, hence, with a larger supply of spores, the possibilities of infection of the white pine are increased accordingly. Spruce logs, containing incipient decay, if left on the ground or on the skidway (Fig. 2) after a logging operation, soon produce a great many sporophores (Fig. 3) and become an important source of infection for neighboring timber. If middle-aged or maturing stands are nearby, partially decayed logs should be removed or burned. Although it is just as logical to believe that spores produced on logs of northern white pine may infect spruce, the likelihood of this is not great. Sporophores of *Fomes pini* rarely occur on pine logs, hence felled pine timber left in the forest would not become an important source of infection.

In any spruce felling operation, apparently sound trees with pocket-rotted heartwood are commonly encountered (Fig. 1). These trees are often left standing and constitute a source of infection for many years, since sporophores continue to be produced. If they are not blown down before the end of another rotation, they continue to be a source of infection when the next crop of timber is nearing maturity and therefore at a highly susceptible age. If spruce or another species susceptible to *Fomes pini* will form the reproduction, it would seem advisable to fell all these decayed trees and leave them in the forest. The fallen timber would bear a great many sporophores but only for a few years. During this time, the reproduction is young and resistant to *Fomes pini* and, hence, there would be slight possibility of any large amount of infection.

SUMMARY

1. A list of 59 hosts of *Fomes pini* (Thore) Lloyd (*Trametes pini* [Thore] Fries) is given. Collections are recorded from 31 states of the United States and 21 foreign countries.

2. By microscopic analysis of decayed stems of living red spruce, *Fomes pini* was found to exist only as a saprophyte in the heartwood.

3. It has been shown that temperature has a direct influence on sporulation.

4. Basidiospores of *Fomes pini* are cast most abundantly during 2 short periods in spring and late fall. The periods of high sporulation were concurrent with rises in temperature above 50° F. following a period of cool but not freezing weather. Very light sporulation continued at all times when the average weekly temperature was above 32° F.

5. Continuous temperature above 50° F. resulted in growth of hyphae in the tubes of the sporophore and the development of a new tube layer.

6. The germination of basidiospores of *Fomes pini* was favorably influenced by a high sugar content of the substratum. Germination reached 93.2 per cent on malt agar.

7. Spore germination was also influenced by the acidity of the substratum within a narrow range. High germination was secured only between 5.0 and 6.0 pH. No germination was obtained on alkaline substrata.

8. Spores germinated upon thin sections of pine and spruce wood.

9. *Fomes pini* was cultured on 24 substrata. Those with a high sugar content proved the more favorable for a rapid and dense growth of mycelium.

10. The hydrogen ion concentration within wide limits was of little influence upon mycelial growth.

11. The mycelium grew at temperatures ranging from 6° C. to 30° C., with an optimum temperature near 25° C.

12. Exposure to light coming through window glass caused a darkening of the mycelium. Exposure to the ultra violet rays in sunlight, in addition to the visible spectrum, caused a further darkening of the mycelium and suppressing of aerial hyphae.

13. Pocket rot was produced in the wood of *Picea rubra* Link by cultures obtained from sporophores collected on *Pinus strobus* L., *Pinus monticola* D. Don., and *Picea rubra* Link.

14. The extent of decay in spruce judged by loss in specific gravity and crushing strength showed as great variation when produced by cultures from the same host as that produced by cultures from different hosts.

15. The different types of decay associated with *Fomes pini* commonly called red rot, pocket rot, and ring scale, were produced in different woods by a subculture from one individual mycelium. This indicates that these various types of decay are entirely due to differences in the host.

This investigation was begun under the direction of the late Dr. L. H. Pennington to whom the author is indebted for inspirational guidance. The author also wishes to express his gratitude to Dr. R. R. Hirt for assuming direction of this study and for advice throughout the investigation, and to Dr. H. F. A. Meier for his active interest and kindly criticism.

Acknowledgments are also due to Mr. C. I. Jones for taking daily readings during the sporulation studies and to Mr. H. Hopp for assistance in making photographs.

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